

Dependencies between competition and predation - and its consequences for initial value sensitivity

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Abstract

We commence with a discussion of dependencies between various processes in discrete consumer-resource models. Two basic models are formulated. These models are closely related and differ in terms of which dependencies are assumed only. The models can be regarded as hybrids of the Lotka-Volterra model, the Beverton-Holt model and the Nicholson-Bailey model.

A complete stability analysis of the equilibria is given with the conclusion that the stability properties of these models are closely related to Gause-type predator-prey systems.

The numerical part of our analysis brings out remarkable qualitative differences concerning the initial value sensitivity of the oscillations of the two basic models. These differences can neither be brought to light by a study of limiting cases, nor by equilibrium analysis. The actual reasons behind these results remain a delicate mathematical question.

Properties associated with the time-series directly, like mean amplitudes and dominating periods, did not show the same differences.

Key words: Discrete dynamical system, Intra-specific competition, Lyapunov exponent, Hopf-bifurcation, Beverton-Holt model, Nicholson-Bailey model, Lotka-Volterra system, Gause-type predator-prey system.

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1 Introduction

In my thesis, Lindström (1994), two papers about discrete ecological modeling were included. In the first paper, Gyllenberg, Hanski and Lindström (1996), a discrete model for predator-prey interactions was developed. In the derivation of this model, the death-processes of the Lotka-Volterra system, Lotka (1925) and Volterra (1926) were considered as continuous processes and the birth-processes were considered as discrete events. Actually, one can show that a Lotka-Volterra system exhibiting discrete births, takes the form,

$$\begin{aligned} X' &= \beta X e^{-Y}, \\ Y' &= M(1 - e^{-Y})X + (1 - \delta)Y. \end{aligned} \tag{1}$$

As $\delta \rightarrow 1$, the above model reduces to the Nicholson-Bailey model, Nicholson and Bailey (1935). I show, in appendix B, that all the equilibria of (1) are unstable. In the light of what is known about the Nicholson-Bailey model, cf. May (1973), these results are expected. Moreover, there is no reason to believe that (1) possesses other bounded solutions, than those at the equilibrium points and the positive part of the y -axis. This states that there are limits of how far we can simplify the underlying processes when we are deriving discrete consumer-resource models. Certain processes must be taken into account, otherwise no reasonable models can be obtained, and we know for the moment, that intra-specific competition among the resource individuals is to be included.

In general, continuous modeling of biological phenomena has extreme advantages in comparison to discrete modeling. On infinitesimally short time intervals, the various processes contributing to population change tend to operate independently, so that we can add their contributions, cf Metz and Diekmann (1986). If we include intra-specific competition in (1), it is not that easy. As an example of comparison, consider the following Gause-type predator-prey system, Gause (1934),

$$\dot{x} = rx - c_1x - dx^2 - \frac{axy}{1 + abx}, \tag{2}$$

$$\dot{y} = \frac{maxy}{1 + abx} - c_2y. \tag{3}$$

In (2), the first term describes the growth of the prey, in the absence of natural death, competition and predation. The second term describes the natural

death, the third term the competition among prey, and the last term describes the predation process, according to the Holling II functional response, Holling (1959). In (3), the first term describes the growth of the predator, and it is assumed that a fraction of the consumed prey-biomass is converted to predator-biomass. The second term in (3) describes the natural death among predators.

If we know how the different processes contribute to population change, it is in general, as simple as in the case (2)-(3), to write a differential equation model for the changes on infinitesimally short time intervals. As the processes act independently, we simply add their contributions.

The situation is completely different in the discrete case (1). First, a discrete single species model allows for representation of more types of competition, than the corresponding continuous single species models. For instance, non-monotonic discrete single species models, like the Ricker (1954)-model, do not have any relations to one-dimensional continuous competition models, cf. Clark (1990, first edition 1976). Mathematically, this is due to the basic local existence and uniqueness theorem for ordinary differential equations. Biologically, in any competition model, the population must be divided, at least into losers and winners. Such a division, can for instance be found in Hanski (1989). He divided the individuals in a competing population into floaters and residents. Residents are individuals, which have a place in the society, giving them possibilities to reproduce. Floaters are individuals, which have either not found such a place or lost this place. This division makes sense, since according to Maynard Smith and Price (1973) and Maynard Smith (1974) intra-specific competition is rarely lethal and therefore floaters, which have experiences of one or several intra-specific combats remain in the population. Since the floaters must live on more barren habitats and the residents must care for their offspring, we might assume that residents and floaters are equally vulnerable to predation. This gives possibilities to consider predation as a process, which occurs independently of intra-specific competition.

Vice versa, the situation is different. In contrast to intra-specific competition, predation certainly removes individuals from the population. As the predation process goes on, the conditions for intra-specific competition change and we must ask under what conditions this must be taken into account. This question is closely related to the notion of scramble- and contest-competition, Nicholson (1954). Scramble-type competition is most typical, when dung, car-

rion and stored products are exploited, cf. Hassell (1976). That is, scramble-type competition contains an element of competition against time or bad environmental conditions and efficiency is promoted rather than competition against other individuals. If this type of competition actually is against time, for instance, if successful reproduction can be made only during a very short period in the beginning of the growing season, this gives possibilities to consider competition as a process acting independently from predation. This is a part of the content of our work in Gyllenberg et. al. (1996). Here the Ricker (1954)-type competition was studied.

When the competition-type is contest, defense is promoted, not efficiency. In its pure sense, this kind of competition is incompatible with the assumption of a short competition period in the beginning of the season, cf. our second paper, Gyllenberg, Hanski and Lindström (1997). Hence contest-type competition does *not* occur independently of predation. However, this type of competition does allow certain other simplifications, not allowed in the scramble-case. In this case, the discrete single-species competition model is monotonous, and a representation with a one-dimensional differential equation is possible. Here, we shall use this simplification to derive a discrete consumer-resource model, which is based on (1), and includes the logistic contest-type competition in (2)-(3).

In this paper we are going to proceed as follows. Our main model is derived in section 2. The obtained model contains expressions involving exponential integrals and the beginning of section 3 is devoted to extract the basic properties of these expressions. After this, a reference model based on the *false* assumption that competition and predation act as independent processes is stated. In the main theoretical part we prove with mathematical rigor that the local stability properties of these two models are qualitatively identical and remind about the corresponding properties of continuous Gause-type predator-prey systems, (2)-(3). Up to our knowledge, no such stability analysis have been done before. In some limiting cases, our main model does not contain special functions. In section 4, we show that no qualitative differences, between the dependent and the independent case, can be discovered in these limiting cases, either. We go on with a numerical study of the complete system. In this case remarkable dynamical differences between the dependent and the independent case are detected, which neither can be observed by a study of limiting cases nor by equilibrium analysis. The proofs can be found in appendix A.

2 Derivation of the model

As concluded in section 1 and appendix B, there are no reasons to believe, that the discrete Lotka-Volterra model (1) can possess bounded solutions, other than the non-stable ones located at the two equilibrium points and the y -axis. Therefore intra-specific competition in the resource population must be included in some sense. In Gyllenberg et. al. (1996), we showed how a short phase of scramble competition in the beginning of the season can be included in (1). In this section, I build up the corresponding model with contest-type competition in the resource population. As noted in section 1, the assumption of contest-type competition is, in its pure sense, incompatible with a short competition phase in the beginning of the season, so competition is dependent from predation. Therefore the derivation presented below contains new elements.

As earlier, we start by integrating the death-processes of the Lotka-Volterra equations. If we assume that the resource-abundance is given by x and the consumer-abundance is given by y during the season, we get,

$$\begin{aligned}\dot{x} &= -axy, \\ \dot{y} &= -cy.\end{aligned}\tag{4}$$

It is justified to leave out the natural death rate of the resource, since we shall assume that the resource is semelparous. Integration of the system (4) of ordinary differential equations gives

$$x(t) = x_0 \exp\left(-\frac{ay_0}{c}(1 - e^{-ct})\right),\tag{5}$$

$$y(t) = y_0 \exp(-ct).\tag{6}$$

We proceed to the calculation of the part of the resource population, which is able to reproduce. In concordance with (2)-(3), we shall assume that they are given by the Bernoulli equation

$$\dot{x}_R = -Kx_R^2 - ax_Ry(t).\tag{7}$$

Put

$$\text{Ei}(x) = \int_{-\infty}^x \frac{\exp(\xi)}{\xi} d\xi.$$

The integral is evaluated as a Cauchy principal value. Equation (7) can be solved, and its solutions are given by

$$x_R(t) = \frac{x_0 \exp\left(-\frac{ay_0}{c}(1 - e^{-ct})\right)}{1 + \frac{Kx_0}{c} \exp\left(-\frac{ay_0}{c}\right) \left(\text{Ei}\left(\frac{ay_0}{c}\right) - \text{Ei}\left(\frac{ay_0}{c}e^{-ct}\right)\right)}. \quad (8)$$

Now assume that these resource-individuals, reproduce with a mean of β offspring at the time-instant T . Simultaneously we assume that, a fraction of the consumed resource-biomass will be converted into consumer-biomass at the time-instant T . We take into account that only $y_0 \exp(-cT)$ consumers are alive at this time instant. Next assume semelparity for the resource and iteroparity for the consumer. We get

$$\begin{aligned} x(T) &= \frac{\beta x_0 \exp\left(-\frac{ay_0}{c}(1 - e^{-cT})\right)}{1 + \frac{Kx_0}{c} \exp\left(-\frac{ay_0}{c}\right) \left(\text{Ei}\left(\frac{ay_0}{c}\right) - \text{Ei}\left(\frac{ay_0}{c}e^{-cT}\right)\right)}, \\ y(T) &= mx_0 e^{-cT} \left(1 - \exp\left(-\frac{ay_0}{c}(1 - e^{-cT})\right)\right) + e^{-cT} y_0. \end{aligned} \quad (9)$$

Note that iteroparity for the resource cannot be assumed by replacing β with $\beta + 1$, because of two reasons. First, we must assume a natural death-rate for the resource in this case, and this will modify the denominator in (9) considerably. Secondly, resource individuals of different age classes are seldom equally vulnerable to predation.

Next we do some transformations. More specifically, we put

$$\begin{aligned} X &= KT x_0, \\ Y &= \frac{ay_0}{c}(1 - e^{-cT}), \\ M &= \frac{ame^{-cT}(1 - e^{-cT})}{cKT}, \\ H(\alpha, \rho) &= -\frac{1}{\log \alpha} \exp(-\rho) (\text{Ei}(\rho) - \text{Ei}(\alpha\rho)), \\ \delta &= 1 - e^{-cT} \end{aligned}$$

and arrive in

$$\begin{aligned} X' &= \frac{\beta X \exp(-Y)}{1 + XH\left(1 - \delta, \frac{Y}{\delta}\right)}, \\ Y' &= MX(1 - \exp(-Y)) + (1 - \delta)Y. \end{aligned} \quad (10)$$

We have reduced the number of parameters from five to three. The parameters, which are left in the model are β , δ and M .

3 Dependencies and local dynamics

Our main model (10) contains expressions involving exponential integrals and in the first part of this section we shall prove that these expressions behave as expected. This is the main content of proposition 1. After this we state a reference model, which contains the *false* assumption that competition and predation act as independent processes. We proceed with a complete analysis of the equilibria of our main model (10) and the reference model. The result is that these two models are surprisingly equal, as far as the properties of the equilibria are considered.

The following proposition proves that the function $H(1 - \delta, Y/\delta)$ behaves as expected. Moreover, several important limiting properties of this function are stated. Before stating proposition 1, we formulate a couple of lemmas, which simplify the proof of the proposition.

Lemma 1 *If $0 < \delta < 1$, then $\delta < -\log(1 - \delta) < \delta/(1 - \delta)$.*

Lemma 2 (Chebyshev's inequality) *Let f and g be two functions, which are integrable and monotone in the same sense on $]a, b[$ and let p be a positive integrable function on the same interval. Then*

$$\int_a^b p(\xi)f(\xi)g(\xi)d\xi \int_a^b p(\xi)d\xi \geq \int_a^b p(\xi)f(\xi)d\xi \int_a^b p(\xi)g(\xi)d\xi, \quad (11)$$

with equality if and only if one of the functions f , g reduces to a constant. If f and g are monotone in the opposite sense, inequality (11) reverses.

Proposition 1 *Assume that $\beta > 1$, $0 < \delta < 1$, $0 < \rho < \infty$, $Y > 0$ and put $\kappa(Y) = (1 - \exp(-Y))/Y$. The function H has the following properties*

- (a) $\lim_{Y \rightarrow 0} H(1 - \delta, Y/\delta) = 1$,
- (b) $\lim_{Y \rightarrow \infty} YH(1 - \delta, Y/\delta) = -\frac{\delta}{\log(1-\delta)}$,
- (c) $\lim_{\delta \rightarrow 0} H(1 - \delta, Y/\delta) = \kappa(Y)$,

- (d) $\lim_{\delta \rightarrow 0} H(1 - \delta, \rho) = 1$,
- (e) $\lim_{\delta \rightarrow 1} H(1 - \delta, Y/\delta) = e^{-Y}$.
- (f) *The function $H(1 - \delta, Y/\delta)$ is, considered as a function of Y , decreasing,*
- (g) $e^{-Y} < H(1 - \delta, Y/\delta) < \kappa(Y)$,
- (h) $\frac{\beta e^{-Y} - 1}{\kappa(Y)} < \frac{\beta e^{-Y} - 1}{H(1 - \delta, Y/\delta)} < \beta - e^Y$.
- (i) *The function $\frac{\beta e^{-Y} - 1}{H(1 - \delta, Y/\delta)}$ is, considered as a function of Y , decreasing.*

Remarks

- (i) It follows from (b) that $\lim_{Y \rightarrow \infty} H(1 - \delta, Y/\delta) = 0$.
- (ii) The statements, (c) and (d), imply that the change $\eta = Y/\delta$ in the model (10) is not allowed.
- (iii) The first inequality of (g) implies that the solutions of (10) are positive and bounded.

Next we proceed to the local dynamical properties of our main model (10). The main bifurcation parameter is β . For $0 < \beta < 1$, the model predicts that the consumer and the resource go extinct. For $1 < \beta < 1 + \delta/M$, the resource is persistent, but the consumer is not. Theorem 1 below, will state that, for moderate values of β , with $\beta > 1 + \delta/M$, the resource and consumer are persistent and the coexistence is, at least locally, stable. Similarly, theorem 1 will state, that for high values of β , none of the equilibria are stable and the consumer and the resource populations must, by remark (iii) above, possess oscillatory coexistence. Thus, the dynamical properties of the system (10) remind a lot of the dynamical properties of the well-known continuous consumer-resource system (2)-(3). In the rest of this paper we shall study cases when both species are persistent only (ie. $\beta > 1 + \delta/M$), since the other cases can be studied with methods considerably simpler than those alluded to below. The following lemma is formulated for a class of systems, larger than the class under consideration here. It will be useful in the proofs of the local stability properties of the system (10) and the reference system, which will be introduced later in this section.

Lemma 3 Consider the general consumer-resource system

$$\begin{aligned} X' &= Xf(X, Y), \\ Y' &= Yg(X, Y). \end{aligned} \tag{12}$$

Assume that

- (i) $f, g \in C^1(\mathbf{R}_+^2)$,
- (ii) $\bar{X}f_X(\bar{X}, \bar{Y}) + \bar{Y}g_Y(\bar{X}, \bar{Y}) > -2$,
- (iii) $\bar{X}\bar{Y} \left(f_X(\bar{X}, \bar{Y})g_Y(\bar{X}, \bar{Y}) - f_Y(\bar{X}, \bar{Y})g_X(\bar{X}, \bar{Y}) \right) > 0$.

Then the interior fixed point (\bar{X}, \bar{Y}) is locally stable if

$$\begin{aligned} \bar{X}f_X(\bar{X}, \bar{Y}) + \bar{Y}g_Y(\bar{X}, \bar{Y}) < \\ -\bar{X}\bar{Y} \left(f_X(\bar{X}, \bar{Y})g_Y(\bar{X}, \bar{Y}) - f_Y(\bar{X}, \bar{Y})g_X(\bar{X}, \bar{Y}) \right) \end{aligned} \tag{13}$$

and unstable if the converse inequality holds. Moreover, equality in (13) corresponds to a discrete Hopf-bifurcation, except for at a few exceptional cases of strong resonance.

Equality in (iii) above, corresponds to a saddle-node bifurcation, but equality in (ii) needs not correspond to a period-doubling bifurcation. Loosely speaking, a period-doubling bifurcation occurs if the inequality in (ii) is violated much. The expression in (iii) has a nice geometrical interpretation. By the formula for implicit derivation, it states how the level curves $f(X, Y) = 1$ and $g(X, Y) = 1$ intersect at (\bar{X}, \bar{Y}) .

In the next theorem we return to our main system (10). To large extent, the theorem is proved by a check of the conditions of lemma 3. But since more about the involved functions are known, we can say more. That is, if β is low, then the interior equilibrium is stable, when it exists. If β is high enough, the system (10) possesses oscillatory coexistence.

Theorem 1 If $\beta > 1 + \delta/M$ the system (10) possesses an unique interior fixed point (X_*, Y_*) . There exists a surface $\beta_*(M, \delta)$ in the parameter space, so that if $1 + \delta/M < \beta < \beta_*(M, \delta)$, then (X_*, Y_*) is locally stable and if $\beta > \beta_*(M, \delta)$, then (X_*, Y_*) is unstable. Furthermore, the bifurcation along the curve $\beta_*(M, \delta)$ is a discrete Hopf-bifurcation, except for at a few exceptional cases of strong resonance.

We assumed in the derivation of the system (10), that competition was dependent of predation. Next we shall start checking the consequences of the *false* assumption that these processes act independently. This corresponds to putting $H(1 - \delta, Y/\delta) = 1$. We get

$$\begin{aligned} X' &= \frac{\beta X \exp(-Y)}{1 + X}, \\ Y' &= MX(1 - \exp(-Y)) + (1 - \delta)Y. \end{aligned} \tag{14}$$

The solutions of (14) are, as the solutions of (10), positive and bounded. The above model will act as our main reference model for independent competition and predation. The next theorem states that the stability properties of the equilibria of the reference system (14) are qualitatively the same as for the system (10).

Theorem 2 *If $\beta > 1 + \delta/M$ the system (14) possesses an unique interior fixed point (X_*, Y_*) . There exists a curve $\beta_*(M, \delta)$ in the parameter space, so that if $1 + \delta/M < \beta < \beta_*(M, \delta)$, then (X_*, Y_*) is locally stable and if $\beta > \beta_*(M, \delta)$, then (X_*, Y_*) is unstable. Furthermore the bifurcation along the curve $\beta_*(M, \delta)$ is a discrete Hopf-bifurcation, except for at a few exceptional cases of strong resonance.*

Theorem 1 and theorem 2 show that no essential differences occur as the systems (10) and (14) undergo the Hopf-bifurcation. In both systems, this bifurcation occurs once, as the parameter value of β is increased. Hence, equilibrium analysis does not reveal any qualitative differences between the two systems.

4 A numerical study

In the preceding section, we made a rigorous comparison of the bifurcations of the equilibria of the systems (10) and (14). As far as equilibria are considered, the systems possess the same qualitative properties, or the same bifurcation sequences with respect to the main parameter β . In this section we are going to show that these similarities are preserved in the nonlinear regimes of the parameter space, as far as a quite simple limiting case is considered, but (surprisingly) not when the complete systems (10) and (14) are compared.

We mention some of the numerical difficulties with these systems, beginning with those not related to the calculation of $H(1 - \delta, Y/\delta)$.

Some serious numerical troubles occur as Y , the number of consumers becomes small. These problems are as visible in the calculation of the time series as they are in the calculation of the Lyapunov exponent. For moderately small values of Y , the formula $1 - \exp(-Y)$ becomes inexact, because of cancelation errors. For smaller values of even worse problems occur, but we commence with the cancelation errors. These errors were eliminated with the Padé-approximation,

$$1 - \exp(-Y) = \begin{cases} 1 - \exp(-Y), & Y > \hat{\varsigma}, \\ \frac{\sum_{i=0}^8 p_i Y^i}{\sum_{i=0}^8 q_i Y^i}, & \varsigma_* < Y < \hat{\varsigma}, \\ Y, & Y < \varsigma_*, \end{cases} \quad (15)$$

where p_i and q_i are given in table 1. The coefficients of the Padé approximation were calculated with the NAG-routine E02RAF. None of these coefficients are negative, hence cancelation errors are completely avoided. The maximal relative error of the approximation (15), with $\varsigma_* = 0$, as a function of $\hat{\varsigma}$ is plotted in figure 1. From this figure, we conclude that an optimal choice of $\hat{\varsigma}$ is 1.6. For this choice, the relative error in (15) is approximately $7 \cdot 10^{-16}$, when $\varsigma_* = 0$. This means that, if we choose $\varsigma_* < 1.4 \cdot 10^{-15}$, then we do not make the approximation formula (15) worse, than it was in the case $\varsigma_* = 0$, in terms of relative errors. In our calculations, we used $\varsigma_* = 2 \cdot 10^{-16}$. The relative error in the vicinity of $2 \cdot 10^{-16}$ is then approximately 10^{-16} , so this choice of ς_* does not influence the validity of our approximation formula (15), which takes the form

$$1 - \exp(-Y) = \begin{cases} 1 - \exp(-Y), & Y > 1.6, \\ \frac{\sum_{i=0}^8 p_i Y^i}{\sum_{i=0}^8 q_i Y^i}, & 2 \cdot 10^{-16} < Y < 1.6, \\ Y, & Y < 2 \cdot 10^{-16}. \end{cases} \quad (16)$$

We are still running into numerical troubles as Y drops below 10^{-323} . These problems can be eliminated, by the observation that second equation of (10) now reads $Y' = M(X + 1 - \delta)Y$, if $Y < 2 \cdot 10^{-16}$. Introducing $\eta = \log Y$, we can rewrite this equation as $\eta' = \log M(X + 1 - \delta) + \log \eta$. We are now able to calculate, at least the time series, for most of the relevant parameter values.

This does not solve the whole problem, since similar problems occur in the calculation of the Lyapunov exponent. These problems are most evident in the vicinity of the saddle point $(\beta - 1, 0)$ in the case $\delta \rightarrow 1$. In this case, proposition 1(e) gives that the system (10) takes the form

$$\begin{aligned} X' &= \frac{\beta X \exp(-Y)}{1 + X \exp(-Y)}, \\ Y' &= MX(1 - \exp(-Y)). \end{aligned} \quad (17)$$

We note that the Jacobian matrix of the system (17) at $(\beta - 1, 0)$ is given by

$$\begin{pmatrix} \frac{1}{\beta} & -\frac{(\beta-1)}{\beta} \\ 0 & M(\beta - 1) \end{pmatrix}. \quad (18)$$

The eigenvector corresponding to the smaller eigenvalue, $1/\beta$ is given by $(1, 0)$ and the eigenvector corresponding to the larger eigenvalue, $M(\beta - 1)$, is given by

$$\left(\frac{-(\beta - 1)}{M\beta(\beta - 1) - 1}, 1 \right).$$

At the origin the Jacobian matrix is given by

$$\begin{pmatrix} \beta & 0 \\ 0 & 0 \end{pmatrix}.$$

Here the eigenvector corresponding to the largest eigenvalue is given by $(1, 0)$ and this eigen-direction is achieved extremely rapidly as the calculation of the Lyapunov exponent proceeds in the vicinity of the origin. Since eigenvectors like $(1, \epsilon)$, where epsilon is less than 10^{-323} , are rounded to $(1, 0)$, the eigen-direction corresponding to the smaller eigenvalue of (18) is achieved exactly, and hence, it takes a long time before the eigen-direction corresponding to the larger eigenvalue of (18) will be approached as the calculation of the Lyapunov exponent proceeds in the vicinity of $(\beta - 1, 0)$. This will give an extensive negative contribution to the Lyapunov exponent. Hence we must keep track on the logarithmic value of the second component of the eigenvector here, too.

We must simultaneously ask, whether such extreme parameter values have a significant biological importance. First, we saw that the consumer-population dropped down to values below 10^{-323} . Then, under quite similar

conditions, we got problems with the calculation of the Lyapunov-exponent. Under any conditions, the deterministic approximation cannot remain valid under these circumstances. Furthermore, a biological population, which drops regularly to extremely low densities for long periods is not very persistent. Hence, we cannot expect any observation of this kind in nature. Hence, we are going to draw just one conclusion in these regions of the parameter parameter space. This is that populations in the extremely nonlinear parts of the parameter-plane (β and M large) are not especially likely to be observed.

After the removal of these numerical difficulties, we compared the qualitative properties of the system (17) numerically with the system

$$\begin{aligned} X' &= \frac{\beta X \exp(-Y)}{1 + X}, \\ Y' &= M(1 - \exp(-Y))X. \end{aligned} \tag{19}$$

System (19) is constructed by taking the limit of (14) as $\delta \rightarrow 1$. The results in the case $M = 3.5$ for $\beta = 1.0 \dots 6.0$ are collected in figure 2. Throughout this figure, the results for the system (17) are denoted with a solid line, whereas the corresponding results for the system (19) are denoted by a dotted line. First we check the Figure 2(a). Here we plotted the mean amplitude (measured in log-co-ordinates) of the oscillations. The diagram shows a stabilizing effect in the system (19), in comparison to the system (17). This is actually what is to be expected. In figure 2(c) the dominating period is plotted. This is the period corresponding to the maximum of the Fourier-spectrum. Here the assumption of independent competition and predation has a slight stabilizing effect, too. In figure 2(b), the periods, if any below 2048 is found, are shown. This figure should be compared with figure 2(d), where the Lyapunov exponent of the oscillation is calculated. The oscillations of the system (17) are remarkably more sensitive to initial conditions, than the corresponding oscillations of (19), though the general patterns for increasing β are similar. Both systems undergo a transition to chaos after the Hopf-bifurcation, as predicted by Aronson, Chory, Hall and McGehee (1982).

We did corresponding experiments for several values of M . In general, if M was increased, both the Hopf-bifurcation and the transition to chaos occurred more rapidly. For very small M , the interior fixed point could be stable for very high β .

We proceed with an analysis of the complete systems, (10) and (14). Here, the main additional numerical difficulties are related to the calculation

of $H(1 - \delta, Y/\delta)$. This expression involves exponential integrals and a quite efficient and accurate algorithm for exponential integrals has been implemented by Press, Teukolsky, Vetterling and Flannery (1992). I modified their code slightly and calculated,

$$\frac{x \text{Ei}(x)}{\exp(x)},$$

instead of $\text{Ei}(x)$. A direct calculation of $\text{Ei}(x)$ causes a rapid overflow, and this is unnecessary, since $\text{Ei}(x)$ is always multiplied with a factor of order $\exp(-x)$.

The results are collected in figure 3. Throughout the figure, the results for the system (10) are denoted by solid line, whereas the dotted lines represent the corresponding results for the system (14). We note that the changes in the amplitude and the dominating periods obey the same patterns as in the case $\delta = 1$, but the growth of the amplitudes is more limited. The most remarkable difference, was that the transition to chaos after the Hopf-bifurcation, occurred as in the limiting case $\delta = 1$, in the dependent case, but not in the independent case (at least not for moderate values of β and M), see figure 3(d). The differences in the amplitudes can not explain the differences in initial value sensitivity.

To see how general this observation was, we plotted figure 4. Here we plotted different observations in the (δ, β) parameter-plane, with δ on the horizontal axis and β on the vertical axis. Green color corresponds to extinction of the consumer. White areas correspond to persistent, non-oscillating consumer and resource populations. Blue dots correspond to solutions with approximately zero Lyapunov exponent. These solutions can be bifurcating or quasi-periodic. Yellow dots correspond to periodic solutions, and a period below 2048 is found. Cyan dots correspond to negative Lyapunov exponents, but no period below 2048 was found. Finally, red dots correspond to chaotic solutions. The main numerical comparison between the systems (10) and (14) is shown in the figures 4(a) and 4(b). Over the whole range of parameter values, a transition to chaos after the Hopf-bifurcation occurs in the case (10). This transition occurs approximately as β exceeds 3.5...4.5, see figure 4(a). As predicted in the case (19), the same transition to chaos should occur for the system (14) in the vicinity of $\delta = 1$. This is actually the case, cf. figure 4(c), but for most of the parameter values this transition does not occur, figure 4(b). Some other transition does occur, and we magnified the rectangle

in figure 4(b), in order to check what happens on a finer scale. The result is plotted in figure 4(d). This figure shows that no new areas with chaotic oscillations occur, although some dispersed chaotic solutions can be detected. This transition is more a transition from quasi- or long-periodic behavior, to oscillations with shorter periods. Further numerical experiments have shown that we do not find larger regimes with chaotic oscillations in the system (14) for any moderate values of β , other than those already found in the vicinity of $\delta = 1$.

It can be a delicate mathematical question to check, why the transition to chaotic behavior did not occur in the independent case, since this is a good example how real qualitative differences between approximating systems and real systems can arise.

5 Summary

In this paper, qualitative differences concerning the initial value sensitivity of the oscillations of the models

$$\begin{aligned} X' &= \frac{\beta X \exp(-Y)}{1 - X \frac{1}{\log(1-\delta)} \exp\left(-\frac{Y}{\delta}\right) \left(\text{Ei}\left(\frac{Y}{\delta}\right) - \text{Ei}\left((1-\delta)\frac{Y}{\delta}\right)\right)}, \\ Y' &= MX(1 - \exp(-Y)) + (1 - \delta)Y \end{aligned} \quad (20)$$

and

$$\begin{aligned} X' &= \frac{\beta X \exp(-Y)}{1 + X}, \\ Y' &= MX(1 - \exp(-Y)) + (1 - \delta)Y, \end{aligned} \quad (21)$$

were reported. Both models are based on the discrete Lotka-Volterra model (1), the difference is that intra-specific competition is assumed independent from predation in (21). If $Y \rightarrow 0$, both models reduce to the Beverton-Holt (1957) model. A complete local stability analysis is given and both models remind, a far as local stability is considered, about the Gause-type predator-prey systems.

The limiting case $\delta \rightarrow 1$ is given special attention. In this case the above models differ as much as possible from each other, and the denominator in (20) takes a particularly simple form. This case did not possess the differences

alluded to above. Therefore care must be exercised when deriving discrete ecological models. The models (20) and (21) are closely related, and their qualitative differences can neither be brought to light by a study of limiting cases, nor by equilibrium analysis.

The main differences were observed in the initial value sensitivity of the oscillations. The transition to chaos in (21), did not occur or occurred essentially slower than in the model (20). Such differences were not observed in properties associated with the time series directly, like mean amplitudes and dominating periods of the oscillations. Here, the differences corroborated what was expected only, ie the oscillations of (20) had slightly larger mean amplitudes and dominating periods than the corresponding oscillations of (21).

A Proofs

Proof of lemma 1 The lemma follows, since

$$\int_{\frac{1-\delta}{\delta}}^{\frac{1}{\delta}} \frac{d\xi}{\xi} = -\log(1-\delta) \quad (22)$$

and $1/\xi$ is strictly decreasing. \square

Proof of lemma 2 A complete listing of various proofs of this lemma as well as historical remarks, were given by Heinig and Maligranda (1991). Here one of the proofs listed there is given. If f and g are monotone in the same sense, then

$$p(s)p(t)(f(s) - f(t))(g(s) - g(t)) \geq 0, \quad (23)$$

for $a \leq s \leq b$ and $a \leq t \leq b$. If they are monotone in the opposite sense, the inequality (23) reverses. Integration of (23) gives

$$\begin{aligned} 0 &\leq \int_a^b \int_a^b p(s)p(t)(f(s) - f(t))(g(s) - g(t))dsdt \\ &= \int_a^b p(t)dt \int_a^b p(s)f(s)g(s)ds - \int_a^b p(t)f(t)dt \int_a^b p(s)g(s)ds - \\ &\quad \int_a^b p(s)f(s)ds \int_a^b p(t)g(t)dt + \int_a^b p(s)ds \int_a^b p(t)f(t)g(t)dt \\ &= 2 \left(\int_a^b p(s)ds \int_a^b p(s)f(s)g(s)ds - \int_a^b p(s)f(s)ds \int_a^b p(s)g(s)ds \right). \end{aligned}$$

Thus (11) follows. □

Proof of proposition 1 (a) The Maclaurin-expansion

$$\text{Ei}(x) = \gamma + \ln x + \sum_{n=1}^{\infty} \frac{x^n}{nn!}, \quad x > 0, \quad (24)$$

$\gamma =$ Euler's constant, cf. Abramowitz and Stegun (1965), shows that $\text{Ei}(x)$ can be approximated with a logarithm in the vicinity of zero. Hence

$$\begin{aligned} \lim_{Y \rightarrow 0+} H\left(1 - \delta, \frac{Y}{\delta}\right) &= - \lim_{Y \rightarrow 0+} \frac{\exp\left(-\frac{Y}{\delta}\right)}{\log(1 - \delta)} \left(\text{Ei}\left(\frac{Y}{\delta}\right) - \text{Ei}\left(\frac{(1 - \delta)Y}{\delta}\right) \right) \\ &= \lim_{Y \rightarrow 0+} \frac{\exp\left(-\frac{Y}{\delta}\right)}{\log(1 - \delta)} (\log(1 - \delta) + O(Y)) = 1. \end{aligned}$$

(b) In this case we use the asymptotic expansion of $\text{Ei}(x)$,

$$\text{Ei}(x) \sim \frac{\exp(x)}{x} \left(1 + \frac{1!}{x} + \frac{2!}{x^2} + \frac{3!}{x^3} + \dots \right),$$

cf. Cody and Thacher (1969). We get

$$\begin{aligned} \lim_{Y \rightarrow \infty} YH\left(1 - \delta, \frac{Y}{\delta}\right) &= - \lim_{Y \rightarrow \infty} \frac{\delta}{\log(1 - \delta)} \left(1 - \frac{\exp(-Y)}{1 - \delta} + O\left(\frac{\delta}{Y}\right) \right) \\ &= - \frac{\delta}{\log(1 - \delta)}. \end{aligned}$$

(c) The generalized mean value theorem and lemma 1 give

$$\begin{aligned} \lim_{\delta \rightarrow 0+} H(1 - \delta, Y/\delta) &= \lim_{\delta \rightarrow 0+} \frac{\exp\left(-\frac{Y}{\delta}\right)}{-\log(1 - \delta)} \int_{\frac{Y}{\delta} - Y}^{\frac{Y}{\delta}} \frac{\exp(\xi)}{\xi} d\xi \\ &= \lim_{\delta \rightarrow 0+} \frac{\exp\left(-\frac{Y}{\delta}\right)}{-\log(1 - \delta)} \cdot \frac{-\log(1 - \delta)}{Y} \int_{\frac{Y}{\delta} - Y}^{\frac{Y}{\delta}} \exp(\xi) d\xi \\ &= \lim_{\delta \rightarrow 0+} \frac{\exp\left(-\frac{Y}{\delta}\right)}{Y} \left(\exp\left(\frac{Y}{\delta}\right) - \exp\left(\frac{Y}{\delta} - Y\right) \right) \\ &= \kappa(Y). \end{aligned}$$

(d) l' Hospital's rule gives

$$\begin{aligned}\lim_{\delta \rightarrow 0^+} H(1 - \delta, \rho) &= \exp(-\rho) \cdot \lim_{\delta \rightarrow 0^+} \frac{\text{Ei}(\rho) - \text{Ei}((1 - \delta)\rho)}{-\log(1 - \delta)} \\ &= \exp(-\rho) \cdot \lim_{\delta \rightarrow 0^+} \exp((1 - \delta)\rho) \\ &= \lim_{\delta \rightarrow 0^+} \exp(-\delta\rho) = 1.\end{aligned}$$

(e) We have

$$\lim_{\delta \rightarrow 1^-} H\left(1 - \delta, \frac{Y}{\delta}\right) = - \lim_{\delta \rightarrow 1^-} \frac{\exp\left(-\frac{Y}{\delta}\right) \text{Ei}\left(\frac{Y}{\delta}\right)}{\log(1 - \delta)} + \lim_{\delta \rightarrow 1^-} \frac{\exp\left(-\frac{Y}{\delta}\right) \text{Ei}\left(\frac{(1 - \delta)Y}{\delta}\right)}{\log(1 - \delta)}.$$

The first term in the last expression is zero. A similar calculation as in (a), shows that the second term is $\exp(-Y)$.

(f) If $(1 - \delta)Y/\delta < \xi < Y/\delta$, we note that

$$\int_{\frac{(1 - \delta)Y}{\delta}}^{\frac{Y}{\delta}} \frac{\exp(\xi)}{\frac{Y}{\delta}} d\xi < \int_{\frac{(1 - \delta)Y}{\delta}}^{\frac{Y}{\delta}} \frac{\exp(\xi)}{\xi} d\xi. \quad (25)$$

This implies that

$$-\frac{\delta\kappa(Y)}{\log(1 - \delta)} < H\left(1 - \delta, \frac{Y}{\delta}\right).$$

Since the partial derivative with respect to Y of $H(1 - \delta, Y/\delta)$ is given by

$$\frac{\partial}{\partial Y} H\left(1 - \delta, \frac{Y}{\delta}\right) = -\frac{1}{\delta} H\left(1 - \delta, \frac{Y}{\delta}\right) - \frac{\kappa(Y)}{\log(1 - \delta)}, \quad (26)$$

it is negative and we have that $H(1 - \delta, Y/\delta)$ is decreasing, being considered as a function of Y .

(g) To prove the first inequality, we assume $(1 - \delta)Y/\delta < \xi < Y/\delta$. We have $\exp(\xi) > \exp((1 - \delta)Y/\delta)$. By (22), this expression is equivalent to

$$-\frac{1}{\log(1 - \delta)} \exp(\xi) \left(\log\left(\frac{Y}{\delta}\right) - \log\left(\frac{(1 - \delta)Y}{\delta}\right) \right) > \exp\left(\frac{(1 - \delta)Y}{\delta}\right),$$

which, by the generalized mean value theorem is equal to

$$-\frac{1}{\log(1 - \delta)} \int_{\frac{(1 - \delta)Y}{\delta}}^{\frac{Y}{\delta}} \frac{\exp(\xi)}{\xi} d\xi > \exp\left(\frac{(1 - \delta)Y}{\delta}\right),$$

for a properly chosen ξ .

The second inequality is a consequence of lemma 2. In other words, we can rewrite the inequality as

$$\begin{aligned} \int_{\frac{(1-\delta)Y}{\delta}}^{\frac{Y}{\delta}} \frac{\exp(\xi)}{\xi} d\xi &< -\frac{\log(1-\delta)}{Y} \int_{\frac{(1-\delta)Y}{\delta}}^{\frac{Y}{\delta}} \exp(\xi) d\xi \\ &= \frac{1}{Y} \left(\int_{\frac{(1-\delta)Y}{\delta}}^{\frac{Y}{\delta}} \frac{d\xi}{\xi} \right) \cdot \left(\int_{\frac{(1-\delta)Y}{\delta}}^{\frac{Y}{\delta}} \exp(\xi) d\xi \right). \end{aligned}$$

Now choose $a = (1-\delta)Y/\delta$, $b = Y/\delta$, $f(\xi) = \exp(\xi)$, $g(\xi) = 1/\xi$ and $p(\xi) = 1$. Now, p is integrable with $\int_a^b p(\xi) d\xi = Y$ and f, g are monotonic in the opposite direction. This implies (g).

(h) This inequality is a consequence of the inequality in (g).

(i) The nominator of the derivative of this function is given by

$$-\beta e^{-Y} H\left(1-\delta, \frac{Y}{\delta}\right) + (\beta e^{-Y} - 1) \left(\frac{1}{\delta} H\left(1-\delta, \frac{Y}{\delta}\right) + \frac{\kappa(Y)}{\log(1-\delta)} \right). \quad (27)$$

We shall prove that the expression (27) is negative. Lemma 1 gives

$$-\log(1-\delta) < \frac{\delta}{1-\delta}.$$

This implies that

$$\frac{1-\delta}{\delta}(\beta e^{-Y} - 1) - 1 < \frac{\beta e^{-Y} - 1}{-\log(1-\delta)}.$$

Now, by (g)

$$\left(\frac{1-\delta}{\delta}(\beta e^{-Y} - 1) - 1 \right) H\left(1-\delta, \frac{Y}{\delta}\right) < \left(\frac{\beta e^{-Y} - 1}{-\log(1-\delta)} \right) \kappa(Y).$$

A slight reorganization of this inequality implies that (27) is negative. \square

Proof of lemma 3 Since (\bar{X}, \bar{Y}) belongs to the interior of \mathbf{R}_+^2 , we must have $f(\bar{X}, \bar{Y}) = 1$ and $g(\bar{X}, \bar{Y}) = 1$. The Jacobian is given by

$$J(\bar{X}, \bar{Y}) = \begin{pmatrix} 1 + \bar{X} f_X(\bar{X}, \bar{Y}) & \bar{X} f_Y(\bar{X}, \bar{Y}) \\ \bar{Y} g_X(\bar{X}, \bar{Y}) & 1 + \bar{Y} g_Y(\bar{X}, \bar{Y}) \end{pmatrix}.$$

The equilibrium (\bar{X}, \bar{Y}) is stable if and only if

$$-1 + |\text{Tr}J(\bar{X}, \bar{Y})| < \det J(\bar{X}, \bar{Y}) < 1.$$

Now

$$\begin{aligned} \text{Tr}J(\bar{X}, \bar{Y}) &= 2 + \bar{X}f_X(\bar{X}, \bar{Y}) + \bar{Y}g_Y(\bar{X}, \bar{Y}), \\ \det J(\bar{X}, \bar{Y}) &= 1 + \bar{X}f_X^*(\bar{X}, \bar{Y}) + \bar{Y}g_Y(\bar{X}, \bar{Y}) \\ &\quad + \bar{X}\bar{Y} \left(f_X(\bar{X}, \bar{Y})g_Y(\bar{X}, \bar{Y}) - f_Y(\bar{X}, \bar{Y})g_X(\bar{X}, \bar{Y}) \right) \end{aligned}$$

and (\bar{X}, \bar{Y}) is stable if and only if

$$\begin{aligned} -\bar{X}\bar{Y} \left(f_X(\bar{X}, \bar{Y})g_Y(\bar{X}, \bar{Y}) - f_Y(\bar{X}, \bar{Y})g_X(\bar{X}, \bar{Y}) \right) &< 0, \\ \bar{X}f_X(\bar{X}, \bar{Y}) + \bar{Y}g_Y(\bar{X}, \bar{Y}) &< 0, \\ +\bar{X}\bar{Y} \left(f_X(\bar{X}, \bar{Y})g_Y(\bar{X}, \bar{Y}) - f_Y(\bar{X}, \bar{Y})g_X(\bar{X}, \bar{Y}) \right) &< 0, \\ -4 - 2\bar{X}f_X(\bar{X}, \bar{Y}) - 2\bar{Y}g_Y(\bar{X}, \bar{Y}) &< 0, \\ -\bar{X}\bar{Y} \left(f_X(\bar{X}, \bar{Y})g_Y(\bar{X}, \bar{Y}) - f_Y(\bar{X}, \bar{Y})g_X(\bar{X}, \bar{Y}) \right) &< 0. \end{aligned}$$

The above inequalities are true if

$$\begin{aligned} -\bar{X}\bar{Y} \left(f_X(\bar{X}, \bar{Y})g_Y(\bar{X}, \bar{Y}) - f_Y(\bar{X}, \bar{Y})g_X(\bar{X}, \bar{Y}) \right) &< 0, \\ \bar{X}f_X(\bar{X}, \bar{Y}) + \bar{Y}g_Y(\bar{X}, \bar{Y}) &< 0, \\ +\bar{X}\bar{Y} \left(f_X(\bar{X}, \bar{Y})g_Y(\bar{X}, \bar{Y}) - f_Y(\bar{X}, \bar{Y})g_X(\bar{X}, \bar{Y}) \right) &< 0, \\ -4 - 2\bar{X}f_X(\bar{X}, \bar{Y}) - 2\bar{Y}g_Y(\bar{X}, \bar{Y}) &< 0. \end{aligned}$$

The first inequality corresponds to (iii), in the theorem, and the second to (13). The last inequality corresponds to (ii) in the theorem. Approximations were used in the derivation of the last inequality only, hence the equilibrium is unstable when the converse inequality in (13) holds.

Let λ_1 and λ_2 be the eigenvalues of the matrix $J(\bar{X}, \bar{Y})$. If $\det J(\bar{X}, \bar{Y}) = 1$, then $\lambda_1\lambda_2 = 1$. By (ii) and (iii), both eigenvalues are complex conjugates and $|\lambda_i| = 1$, $i = 1, 2$. Hence, equality in (13), corresponds to a discrete Hopf-bifurcation. \square

Proof of theorem 1 We prove first that the interior fixed point (X_*, Y_*) exists and is unique. If we solve the equations

$$\begin{aligned} X_* &= \frac{\beta X_* \exp(-Y_*)}{1 + X_* H(1 - \delta, Y_*/\delta)}, \\ Y_* &= M X_* (1 - \exp(-Y_*)) + (1 - \delta) Y_*, \end{aligned}$$

we obtain

$$X_* = \frac{\beta \exp(-Y_*) - 1}{H(1 - \delta, Y_*/\delta)}, \quad (28)$$

$$X_* = \frac{\delta}{M \kappa(Y_*)}. \quad (29)$$

Call the functions defined by (28)-(29), $f_*(Y)$ and $g_*(Y)$, respectively. By proposition 1(i) function $f_*(Y)$ is strictly decreasing, and by proposition 1(c) and 1(f), the function $g_*(Y)$ is strictly increasing. Both functions are continuous. By proposition 1(a), we have $\lim_{Y \rightarrow 0} f_*(Y) = \beta - 1$ and $\lim_{Y \rightarrow 0} g_*(Y) = \frac{\delta}{M}$. Moreover, $f_*(\log \beta) = 0$ and by proposition 1(b) and (c), $\lim_{Y \rightarrow \infty} g_*(Y) = \infty$. Hence the graphs of the functions f_* and g_* intersect once. This implies that the system (10) has a unique fixed point in the interior of \mathbf{R}_+^2 if $\beta > 1 + \delta/M$.

Assertion (i) of lemma 3 is valid, so we proceed to (ii). By proposition 1(b) and (f)

$$X_* f_X(X_*, Y_*) = -\frac{X_* H(1 - \delta, Y_*/\delta)}{1 + X_* H(1 - \delta, Y_*/\delta)} > -1 \quad (30)$$

and by proposition 1(g) we get

$$Y_* g_Y(X_*, Y_*) = M X_* (e^{-Y_*} - \kappa(Y_*)) = \delta \left(\frac{e^{-Y_*} - \kappa(Y_*)}{\kappa(Y_*)} \right) > -1, \quad (31)$$

hence (ii) is valid and the interior fixed point possesses no period-doubling bifurcations.

We proceed to (iii). By the formula for implicit derivation, the derivatives of the functions $f_*(Y)$ and $g_*(Y)$ calculated at Y_* are given by $-f_Y(X_*, Y_*)/f_X(X_*, Y_*) < 0$ and $-g_Y(X_*, Y_*)/g_X(X_*, Y_*) > 0$, respectively. This implies

$$\frac{f_Y(X_*, Y_*)}{f_X(X_*, Y_*)} > \frac{g_Y(X_*, Y_*)}{g_X(X_*, Y_*)}.$$

We conclude that

$$g_X(X_*, Y_*) = M\kappa(Y_*) > 0 \quad (32)$$

and by (30), we get $f_X(X_*, Y_*) < 0$, hence

$$f_X(X_*, Y_*)g_Y(X_*, Y_*) - g_X(X_*, Y_*)f_Y(X_*, Y_*) > 0$$

and (iii) in lemma 3 holds.

It remains to check under what conditions (13) holds. We note that

$$f_Y(X_*, Y_*) = -1 - \frac{X_* \frac{\partial}{\partial Y} H \left(1 - \delta, \frac{Y_*}{\delta}\right)}{1 + X_* H \left(1 - \delta, \frac{Y_*}{\delta}\right)}$$

and by the equalities in (29), (30), (31) and (32), we obtain

$$\begin{aligned} & \left(M\kappa(Y_*) + \delta H \left(1 - \delta, \frac{Y_*}{d}\right) \right) \left(X_* f_X(X_*, Y_*) + Y_* g_Y(X_*, Y_*) \right. \\ & \left. + X_* Y_* (f_X(X_*, Y_*)g_Y(X_*, Y_*) - f_Y(X_*, Y_*)g_X(X_*, Y_*)) \right) = \\ & -\delta H \left(1 - \delta, \frac{Y_*}{d}\right) + \delta M(1 - \kappa(Y_*)) \\ & + \delta^2 Y_* \left(H \left(1 - \delta, \frac{Y_*}{\delta}\right) + \frac{\partial}{\partial Y} H \left(1 - \delta, \frac{Y_*}{\delta}\right) \right). \end{aligned} \quad (33)$$

The above expression tends to $-\delta < 0$ as $Y_* \rightarrow 0$. We use (26) and proposition 1(b) to show that it tends to $\delta M - \delta^3 / \log(1 - \delta) > 0$ as $Y_* \rightarrow \infty$. The first two terms are increasing functions of Y_* . It remains to check that the last term increases, too. The Y -derivative of the last term above is

$$\delta(1 - \delta)H \left(1 - \delta, \frac{Y_*}{\delta}\right) \left(\frac{Y_*}{\delta} - 1\right) - \frac{\delta^2}{\log(1 - \delta)} \left(1 - \kappa(Y_*)\frac{Y_*}{\delta}\right). \quad (34)$$

We shall show that (34) is positive. We divide the above expression with $-(1 - \delta) \exp(-Y_*/\delta) / \log(1 - \delta) > 0$ and put

$$L(\delta, Y_*) = \delta \left(\int_{\frac{Y_*}{\delta} + Y_*}^{\frac{Y_*}{\delta}} \frac{\exp(\xi)}{\xi} d\xi \left(\frac{Y_*}{\delta} - 1\right) - e^{\frac{Y_*}{\delta}} + \frac{e^{\frac{Y_*}{\delta} - Y_*}}{1 - \delta} \right).$$

From lemma 1 and (24) we get

$$\lim_{Y_* \rightarrow 0} L(\delta, Y_*) = \delta \left(\frac{\delta}{1 - \delta} + \log(1 - \delta) \right) > 0 \quad (35)$$

and from (25) we get

$$L_Y(\delta, Y_*) = \int_{\frac{Y_*}{\delta} - Y_*}^{\frac{Y_*}{\delta}} \frac{\exp(\xi)}{\xi} d\xi - \delta e^{\frac{Y_*}{\delta}} \kappa(Y_*) > 0. \quad (36)$$

By the fundamental theorem of calculus, the inequalities (35) and (36) imply $L(\delta, Y_*) > 0$, which implies that (33) increases from $-\delta < 0$ to $\delta M - \delta^3 / \log(1 - \delta) > 0$ as Y_* increases. Hence, the Hopf bifurcation occurs once as Y_* increases. From (28)-(29) we get that Y_* is a strictly increasing function of β . Thus, the Hopf-bifurcation occurs once as β increases, too. \square

Proof of theorem 2 In this case $H(1 - \delta, Y/\delta) = 1$. We have to modify the arguments of the proof of the theorem 1 in a few cases only. In this case the fixed point is given by

$$X_* = \beta \exp(-Y_*) - 1, \quad (37)$$

$$X_* = \frac{\delta}{M \kappa(Y_*)}. \quad (38)$$

In concordance with the proof of theorem 1, we call the functions defined by (37)-(38), f_* and g_* , respectively. By (29), $g_* = g_*$. Obviously f_* decreases, but not through the arguments alluded to in the preceding proof. Now $\lim_{Y \rightarrow 0} f_*(Y) = \beta - 1$ and $f_*(\log \beta) = 0$. Hence, the fixed point (X_*, Y_*) exists and is unique if $\beta > 1 + \delta/M$. Assertion (i) and (iii) of lemma 3 follow. To prove assertion (ii) of lemma 3, we only have to use (30)-(31) and insert $H(1 - \delta, Y/\delta) = 1$. We proceed to condition (13). In expression (33), we have still not made use of the differential equation (26). Therefore, we can substitute $H(1 - \delta, Y_*/\delta) = 1$ in expression (33). We get

$$-\delta + \delta M(1 - \kappa(Y_*)) + \delta^2 Y_*,$$

which obviously increases from $-\delta$ to $+\infty$ as Y_* increases from 0 to $+\infty$. Using (37)-(38) we get that the Hopf-bifurcation occurs once as β increases. \square

B The discrete Lotka-Volterra system

Lemma 4 *All equilibrium points of the discrete Lotka-Volterra system (1), are unstable if $\beta > 1$.*

Proof The origin is a saddle, and hence, unstable. It is possible to calculate the co-ordinates of the interior equilibrium point. The Jacobian of (1) calculated at these co-ordinates is given by

$$J\left(\frac{\beta\delta \log \beta}{M(\beta-1)}, \log \beta\right) = \begin{pmatrix} 1 & -\frac{\beta\delta \log \beta}{M(\beta-1)} \\ M^{\frac{\beta-1}{\beta}} & \frac{\delta \log \beta}{\beta-1} + 1 - \delta \end{pmatrix}.$$

The determinant of this matrix is given by

$$\frac{-1 + \beta + \delta - \beta\delta + \beta\delta \log \beta}{-1 + \beta}.$$

We shall prove that this expression is greater than one. Since $\beta > 1$, we have

$$\int_1^\beta \log x dx = [x \log x - x]_1^\beta = \beta \log \beta - \beta + 1 > 0.$$

We multiply this expression with δ , add $\beta - 1$ to both sides and divide with $\beta - 1$. We have proved that

$$\frac{-1 + \beta + \delta - \beta\delta + \beta\delta \log \beta}{-1 + \beta} > 1.$$

Hence both fixed points of the discrete Lotka-Volterra system (1) are unstable. \square

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4	A numerical study of the system (10) and the system (14). Parameter values corresponding to chaotic solutions are plotted with red dots, Quasi-periodic and bifurcating solutions are denoted with blue dots, Cyan dots denote periodic solutions, with extremely high periods and yellow dots low periodic solutions (period below 2048). White areas mean stable coexistence and green areas non-persistent consumer populations. (a) Bifurcation diagram of the system (10). (b) Bifurcation diagram of the system (14). (c) Special study of parameter values in the vicinity of $\delta = 1$ in the system (14). (d) Special study of the parameter values in the small rectangle in (b), of the system (14). The parameter δ is plotted on the horizontal axis and the parameter β is plotted on the vertical axis.	33

i	p_i	q_i
0	0.0	1.0
1	1.0	0.500000000145754075
2	$0.145754075475679201 \cdot 10^{-9}$	0.116666666738080557
3	$0.33333333318701769 \cdot 10^{-1}$	$0.166666666827685189 \cdot 10^{-1}$
4	$0.468725058766494840 \cdot 10^{-11}$	$0.160256410474128672 \cdot 10^{-2}$
5	$0.213675213630699912 \cdot 10^{-3}$	$0.106837607029436137 \cdot 10^{-3}$
6	$0.259175818827228621 \cdot 10^{-13}$	$0.485625486734756669 \cdot 10^{-5}$
7	$0.277500277311349342 \cdot 10^{-6}$	$0.138750139143255132 \cdot 10^{-6}$
8	$0.179006913814599511 \cdot 10^{-16}$	$0.192708526707289281 \cdot 10^{-8}$

Table 1: Coefficients of the Padé-approximation (15).

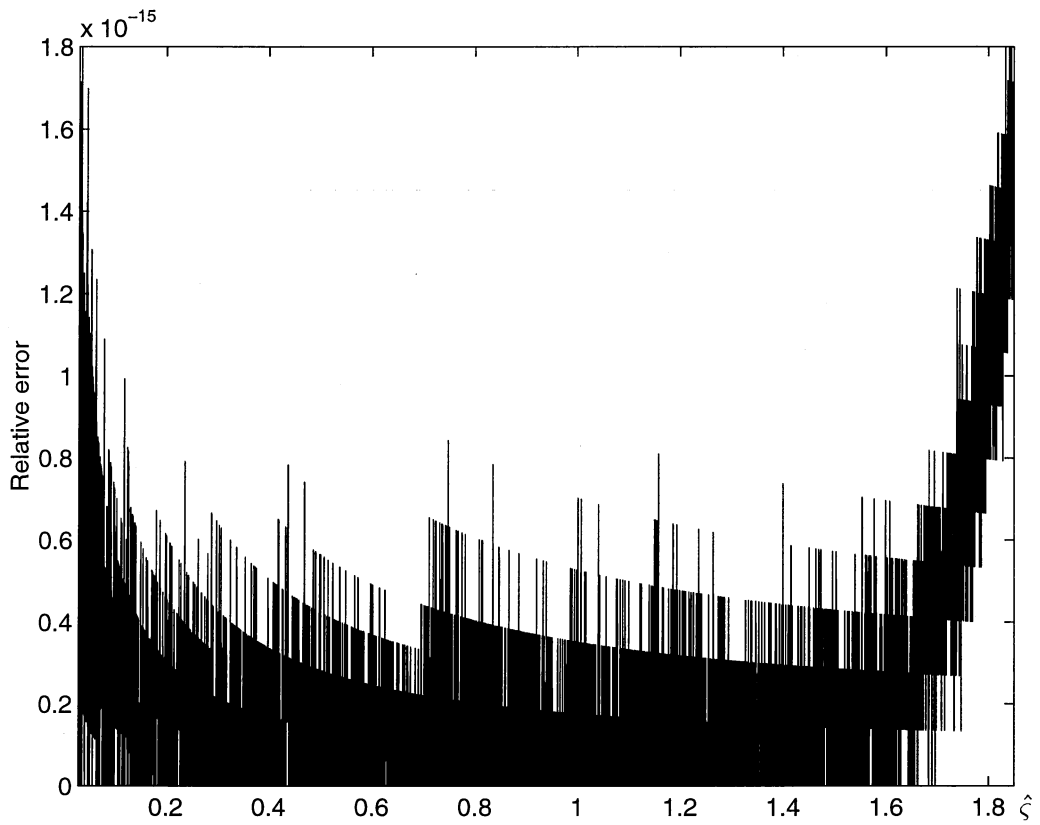


Figure 1: Relative errors in formula (15) for different choices of $\hat{\zeta}$. The value of $\hat{\zeta}$ is plotted at the horizontal axis and the relative error is plotted along the vertical axis.

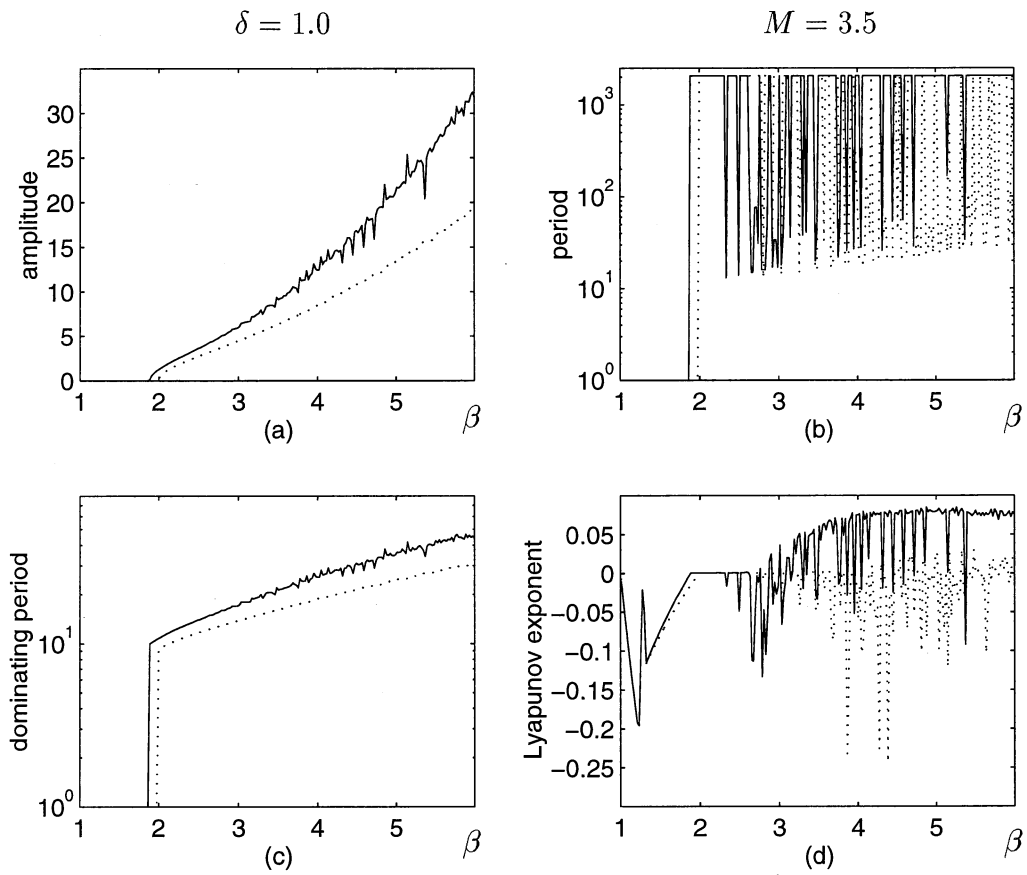


Figure 2: A numerical study of the system (17) (solid line), and the system (19) (dotted line). (a) Mean amplitudes of the oscillations in log-coordinates, (b) periods, if any below 2048, (c) dominating periods, (d) Lyapunov exponents. The values of β are plotted on the horizontal axis.

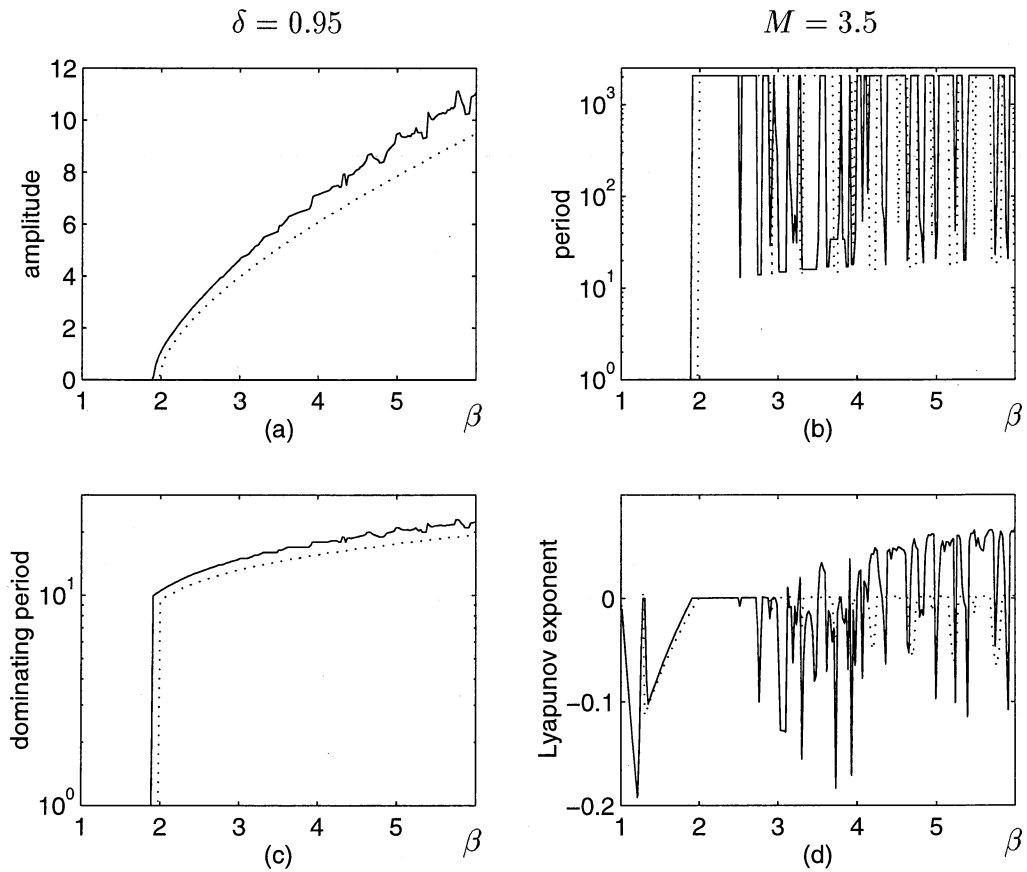


Figure 3: A numerical study of the system (10) (solid line), and the system (14) (dotted line). (a) Mean amplitudes of the oscillations in log-coordinates, (b) periods, if any below 2048, (c) dominating periods, (d) Lyapunov exponents. The values of β are plotted along the horizontal axis.

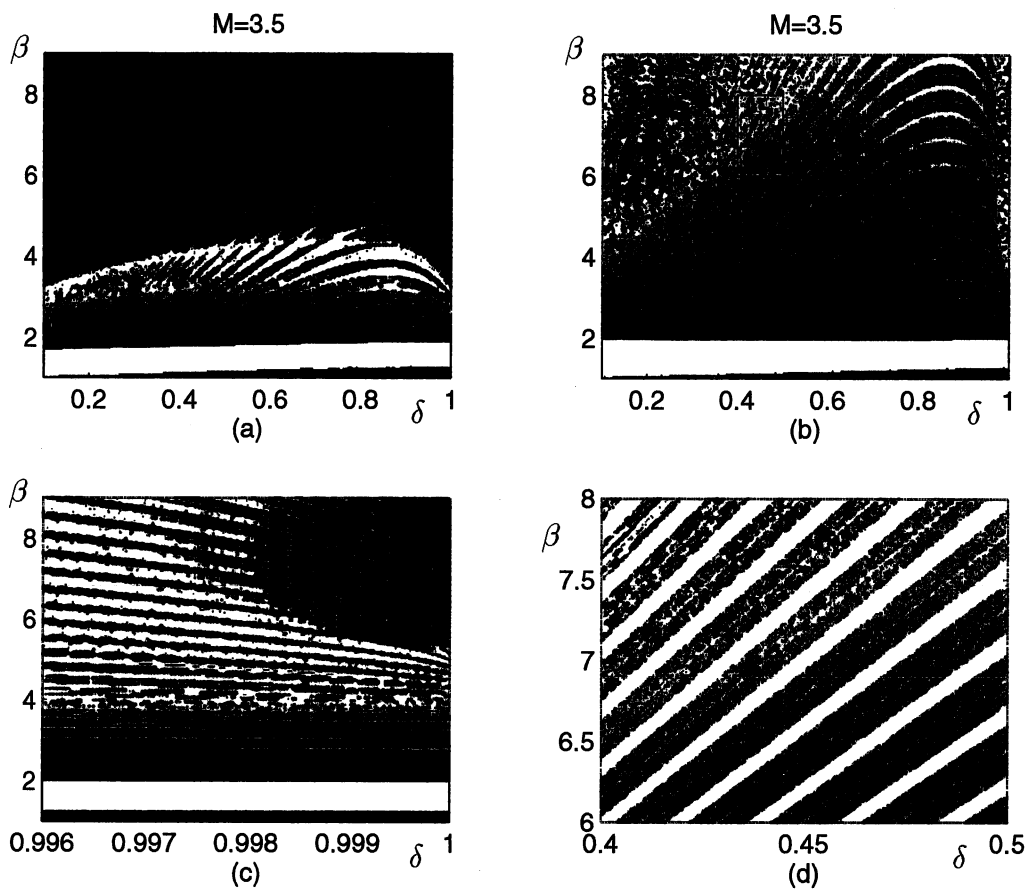


Figure 4: A numerical study of the system (10) and the system (14). Parameter values corresponding to chaotic solutions are plotted with red dots, Quasi-periodic and bifurcating solutions are denoted with blue dots, Cyan dots denote periodic solutions, with extremely high periods and yellow dots low periodic solutions (period below 2048). White areas mean stable coexistence and green areas non-persistent consumer populations. (a) Bifurcation diagram of the system (10). (b) Bifurcation diagram of the system (14). (c) Special study of parameter values in the vicinity of $\delta = 1$ in the system (14). (d) Special study of the parameter values in the small rectangle in (b), of the system (14). The parameter δ is plotted on the horizontal axis and the parameter β is plotted on the vertical axis.

