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F. van den Bosch, O. Diekmann

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EGG-EATING PREDATOR-PREY INTERACTIONS: THE EFFECT OF THE FUNCTIONAL RESPONSE AND OF AGE-STRUCTURE

F. van den Bosch, O. Diekmann

Centre for Mathematics and Computer Science
Kruislaan 413
1098SJ Amsterdam, the Netherlands

ABSTRACT

In this paper we analyse an age-structured predator-prey model in which predators eat only very young prey. The model can be formulated as a system of three Volterra integral equations with an implicitly defined non-linearity. An interpretation of the implicit relation is given. The linearized stability of the steady-states is investigated. It turns out that concentration of the predator on very young individuals is a stabilizing mechanism. Furthermore, it is seen that a compound parameter which is a measure for the efficiency of the predator has a major influence on the stability of the steady-states. If the efficiency of the predator decreases the steady-state can become unstable and oscillations will arise. Furthermore it is seen from the model that the destabilizing effect of a juvenile period is stronger when it concerns the predator than when it concerns the prey species.

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1. INTRODUCTION

Many authors have introduced predator-prey models which take account of realistic biological mechanisms. MURDOCH & OATEN (1975) present a good review of the insight which can be gained from such studies. But still many models suffer from obvious shortcomings, a rather important one being that all individuals of the same species are treated as being equal. Such models ignore the well-known fact that demographic indices such as fecundity and surivival probability as well as properties related to the predation process such as vulnerability or agressivity vary with the age, weight or some other physiological characteristic of the individuals.

Some authors have introduced age-dependent demographic properties into predator prey models (see for instance CUSHING & SALEEM (1982); HASTINGS & WOLLKIND (1982)).

Recently age-dependence in parameters describing the predation process has received some attention. From the biological literature it is known that many predators do not eat all ages of prey indiscriminately. There are, for instance, many well-documented examples where predators eat only the very young individuals or the eggs of the prey. (NIELSON 1980; LE CREN et al. 1977; P.S. DAWSON 1979; A.F. BROWN & M. DIAMOND 1984;). In order to translate this observation into a manageable model GURTIN and LEVINE (1979) introduced the extreme case in which predation only affects the rate of recruitment of the prey. In other words, the predation takes place instantaneously at prey-age zero. This type of interaction is now commonly refered to as an 'egg-eating predator-prey relation'. In continuations of this study many authors have given different forms to the factor with which the birth-rate is reduced to the actual recruitement rate (GURTIN & LEVINE 1979; THOMPSON et al. 1982; COLEMAN & FRAUENTHAL 1983). DIEKMANN et al. (1985) criticize all of these. The mistake that produces wrong results is that in the derivation of the birth-rate-reduction factor rates are treated as numbers. A correct derivation, incorporating a general functional response, is given in DIEKMANN et al. (1985) and subsequently it is used in a model for a cannibalistic species.

In this paper we use the same approach to construct an egg-eating

predator model. We will combine some analytical and numerical work and reveal some robust properties of the model. Analytically the stability of the non-trivial steady-state is studied for the most simple case and for a prey species with a reproductive capacity slightly larger than the critical one. Next we turn to a special case involving step functions for the age specific birth-rates and predation index. The stability boundaries in this case are calculated numerically.

2. THE MODEL

Consider age-structured prey and predator populations with age distributions given by, respectively, $\rho(t,a)$ and $\psi(t,\tau)$. (We shall, for the sake of clarity, systematically denote prey age by a and predator age by τ). The evolution of these distributions is governed by the well-known McKENDRICK equation.

$$\frac{\partial}{\partial t}\rho(t,a) + \frac{\partial}{\partial a}\rho(t,a) = -\nu(t,a)\rho(t,a)$$

(2.1)

$$\frac{\partial}{\partial t}\psi(t,\tau) + \frac{\partial}{\partial \tau}\psi(t,\tau) = -\omega(t,\tau)\psi(t,\tau)$$

With the boundary conditions

(2.2a) $$\rho(t,0) = b_1(t)$$

(2.2b) $$\psi(t,0) = b_2(t).$$

In order to define a complete model we have to specify the birth- and death-rates for both populations.

Let B(a) be the expected number of young produced by a prey individual of age a per unit of time. We assume that the birth rate of the prey is density independent, so we take

(2.3) $$b_1(t) = \int_0^\infty B(a)\rho(t,a)da.$$

The birth rate of the predator does depend on the amount of prey eaten and on the reproductive capacity of the predator. The two quantities of importance here are the attack rate of the predator on the prey and the conversion efficiency of prey, eaten by a predator, into new predators. We will assume that prey-age and predator-age influence each of these quantities independently. The attack rate is given by $G(\tau)C(a)$, where

$C(a)$ = The prey age specific attack rate

$G(\tau)$ = The predator age-specific predation index.

These functions can be normalized in various ways. We will normalize such that $G(\tau) \in [0,1]$ and $G(\tau) = 1$ for at least one τ. The conversion factor is given by $K(\tau)\zeta(a)$, where

$\zeta(a)$ = The maximal number of new predators from a prey of age a

$K(\tau)$ = The predator age-specific reproduction index normalized such that $K(\tau) \in [0,1]$ and $K(\tau) = 1$ for at least one τ.

The birth rate of the predator at a certain time t depends linearly on the total amount of prey eaten at that time. So

$$(2.4) \qquad b_2(t) = \int_0^\infty G(\tau)K(\tau)\psi(t,\tau)d\tau \int_0^\infty \zeta(a)C(a)\rho(t,a)da\ \Phi(c(t)),$$

where $\Phi(c(t))$ is a correction factor which we will explain later on.

For the predator population we assume that the death-rate does only depend on the age of the predator and take:

$$(2.5) \qquad \omega(t,\tau) = \omega(\tau).$$

The death rate of the prey consists of two terms both of which are prey-age specific. The first is the rate of death ($\mu(a)$) due to causes other than predation. The second is the rate of death due to predation.

$$(2.6) \qquad \nu(t,a) = \mu(a) + C(a)Q(t)\Phi(c(t))$$

with

$$(2.7) \qquad Q(t) = \int_0^\infty G(\tau)\psi(t,\tau)d\tau$$

$$(2.8) \qquad c(t) = \int_0^\infty \beta(a)C(a)\rho(t,a)da$$

where

$\mu(a)$ = the age specific death-rate of the prey

$\Phi(c(t))$ = the correction factor for density dependent effects; below we shall interpret Φ as the fraction of the time that a predator spends searching at prey density ρ.

$\beta(a)$ = the prey age specific handling time.

We can interpret Q as the effective number of predators and c as the effective number of potential victims (see below)

The functional response, i.e. the number of prey eaten per predator per unit of time, is now given by

$$(2.9) \qquad R(\rho(t,a)) = \int_0^\infty C(a)\rho(t,a)da \; \Phi(c(t)).$$

We will make the, biologically reasonable, assumption that $c\Phi(c)$ is increasing for $c \geq 0$ and that $\Phi(c)$ is decreasing for $c \geq 0$. Since $CQ\Phi$ occurs as a product in equation (2.6) we can normalize Φ in various ways. We will normalize such that $\Phi(0) = 1$ and $\lim_{c\to\infty} c\Phi(c) = 1$. Here we assume that the limit exists and is finite (As a side remark we mention that the VOLTERRA-LOTKA linear functional response corresponds to the choice $\Phi(c) \equiv 1$)

For instance we can take:

$$(2.10) \qquad \Phi(c(t)) = \frac{1}{1+c(t)}$$

Then the functional response is the age-structured analogue of the Holling type II functional response. This can be seen from the following argument. The total time a predator spends handling prey (T_h) equals the handling time per prey times the total number of catches. The total number of catches equals the attack rate multiplied by the population density and the total time spent searching (T_s). In the age-structured model we get:

$$(2.11) \qquad \int_0^\infty \beta(a)C(a)\rho(t,a)da \; T_s = T_h.$$

So in this context c is the ratio of the time spent handling and the time spent searching and as such it is a convenient measure for the overall prey density. HOLLING argued that the total time available to the predator T is the sum of the total handling time and the searching time ($T = T_s + T_h$). Substitution in (2.11) gives:

$$(2.12) \qquad \frac{T_s}{T} = \frac{1}{1+\int_0^\infty \beta(a)C(a)\rho(t,a)da} = \frac{1}{1+c} .$$

Which is exactly formula (2.10) for the correction factor $\Phi(c)$.

The general model is now complete. It allows for predation varying with the age of the prey and with the age of the predator in an independent manner. Next, we specialize to predation on the utmost young individuals. In the limiting case that we are going to study, the predation takes place instantaneously at a = 0. The basic idea is to let the age interval in which the prey suffers from predation, as described by the support of C(a), tend to zero while at the same time increasing the risk per unit of time of falling a victim to predation in such a way that the total risk, as described by $\theta = \int_0^\infty C(a)da$ remains strictly positive. The parameter θ can be considered as a vulnerability index.

We refer to DIEKMANN et al.(1985) for the technical details of the limit procedure. The limit-model takes the form:

$$(2.13a) \qquad \frac{\partial\rho}{\partial t} + \frac{\partial\rho}{\partial a} = -\mu(a)\rho(t,a)$$

$$(2.13b) \qquad \rho(t,0) = b_1(t)\exp(-\theta Q(t)\Phi(c(t)))$$

$$(2.13c) \qquad \frac{\partial\psi}{\partial t} + \frac{\partial\psi}{\partial\tau} = -\omega(\tau)\psi(t,\tau)$$

$$(2.13d) \qquad \psi(t,0) = b_2(t)$$

where

$$(2.13e) \qquad b_1(t) = \int_0^\infty B(a)\rho(t,a)da$$

$$(2.13f)\qquad b_2(t) = \zeta\beta^{-1}c\Phi(c)\int_0^\infty K(\tau)G(\tau)\psi(t,\tau)d\tau$$

$$(2.13g)\qquad Q(t) = \int_0^\infty G(\tau)\psi(t,\tau)d\tau$$

$$(2.13h)\qquad \frac{c(t)\Phi(c(t))}{\beta} = \frac{b_1(t)}{Q(t)}\,(1-\exp(-\theta Q(t)\Phi(c(t))))$$

with $\zeta = \zeta(0)$ and $\beta = \beta(0)$. For $Q(t) = 0$ the right-hand side of (2.13h) should be interpreted as $\theta b_1(t)\Phi(c(t))$.

From (2.13h) we see that the predation rate is determined by an implicit relation. The left-hand side is equal to the limit of the functional response (2.9). The right-hand side is, indeed, equal to the number of prey eaten per predator per unit of time. Hence (2.13e) is a consistency condition. The assumptions on $c\Phi(c)$ and $\Phi(c)$ ensure that c is uniquely determined as a function of b_1 and Q by this implicit relation.

System (2.13) will be the subject of our analysis in the next paragraph.

3. STEADY-STATES AND STABILITY

By integration along characteristics we can reduce the limit-model to a system of three Volterra-integral equations and one scalar-equation.

$$(3.1)\qquad \begin{cases} b_1(t) = \gamma\displaystyle\int_0^\infty g(a)b_1(t-a)\exp(-\theta Q(t-a)\Phi(c(t-a)))da \\ b_2(t) = \zeta\beta^{-1}\delta c\Phi(c)\displaystyle\int_0^\infty f(\tau)b_2(t-\tau)d\tau \\ Q(t) = \alpha\displaystyle\int_0^\infty h(\tau)b_2(t-\tau)d\tau \\ \dfrac{c(t)\Phi(c(t))}{\beta} = \dfrac{b_1(t)}{Q(t)}\,(1-\exp(-\theta Q(t)\Phi(c(t)))). \end{cases}$$

Where $\gamma g(a) = B(a)e^{-\int_0^a \mu(\sigma)d\sigma}$

$$\delta f(\tau) = G(\tau)K(\tau)e^{-\int_0^\tau \omega(\sigma)d\sigma}$$

$$\alpha h(\tau) = G(\tau)e^{-\int_0^\tau \omega(\sigma)d\sigma}$$

and γ,δ and α are chosen such that $g(a)$, $f(\tau)$, $h(\tau)$ have integral one. Consequently

γ = the expected number of offspring produced by one newly recruited prey individual during the course of its future life.

δ = the expected time a predator spends searching and eating during the whole course of its reproductive life.

α = the expected time a predator spends searching and handling during its entire life.

We will study the existence and local stability of the steady-states of this system. For a treatment of the theory of linearized stability of Volterra convolution integral equations we refer to DIEKMANN & VAN GILS (1984).

Besides the trivial-steady-state

$$(\hat{b}_1,\hat{b}_2,\hat{Q},\hat{c}) = (0,0,0,0)$$

we also find a non-trivial steady-state from:

$$(3.2)\qquad \begin{cases} \hat{c}\Phi(\hat{c}) = \dfrac{\beta}{\zeta\delta} \\ \hat{b}_1 = \hat{c}\,\dfrac{1}{\theta\beta}\,\dfrac{\gamma \ln \gamma}{\gamma-1} \\ \hat{b}_2 = \dfrac{1}{\alpha}\,\dfrac{\ln \gamma}{\theta\Phi(\hat{c})} \\ \hat{Q} = \dfrac{\ln \gamma}{\theta\Phi(\hat{c})} \end{cases}$$

The assumptions on Φ ensure that the first equation has a unique solution (which does not depend on γ!) provided that $\zeta\delta/\beta>1$. From the interpretation of δ and β we see that δ/β is the maximal number of victims a predator can make during the whole course of its life. Multiplying this quantity with the conversion factor ζ gives the maximal number of offspring a predator can have. When $\zeta\delta/\beta<1$ the predator population goes extinct no matter how large the prey population is. We will call $\zeta\delta/\beta$ the efficiency factor of the predator.

In the special case $\Phi(c) = 1/1+c$ we find explicitly

$$\hat{c} = \frac{1}{\frac{\zeta\delta}{\beta} - 1} \quad . \tag{3.3}$$

For $\gamma = 1$ there are also the steady-states

$$\begin{cases} c^* = \beta\theta b_1^* \\ b_1^* \in \mathbb{R}, \text{ arbitrary} \\ b_2^* = 0, \\ Q^* = 0 \end{cases} \tag{3.4}$$

The bifurcation diagram is depicted in Figure 1. Note the vertical bifurcation at $\gamma = 1$.

Linearization of (2.13) about the trivial steady-state yields the characteristic equation

$$\gamma\bar{g}(\lambda) - 1 = 0$$

where

$$\bar{g}(\lambda) = \int_0^\infty e^{-\lambda a} g(a)da$$

and we can conclude that the trivial steady-state is stable if $\gamma < 1$ and unstable if $\gamma > 1$ in accordance with the biological interpretation of γ.

Linearization about the non-trivial steady-state (3.2) yields, after some calculations, the characteristic equation

$$\bar{g}(\lambda)[\bar{h}(\lambda)(1-q)k(\gamma) + (\bar{f}(\lambda)-1)(qk(\gamma)+1)] \tag{3.5}$$

$$-\bar{h}(\lambda)(1-q)m(\gamma) - (\bar{f}(\lambda)-1)(qm(\gamma)+1) = 0$$

where $k(\gamma) = \frac{\ln \gamma}{\gamma - 1} - 1 + \ln \gamma$

$$m(\gamma) = \frac{\ln \gamma}{\gamma - 1} - 1 = k(\gamma) - \ln \gamma$$

and

$$q = -\hat{c}\,\frac{\Phi'(\hat{c})}{\Phi(\hat{c})}.$$

The assumptions about $\Phi(c)$ imply that the parameter q necessarily is confined to the interval (0,1).

For our special case $\Phi(c) = 1/1+c$ we find:

$$q = \frac{\zeta\delta}{\beta}$$

which is the efficiency factor of the predator as we have defined earlier. (As an aside note that $\Phi(c) \equiv 1$ yields $q = 0$)

Equation (3.5) is rather unwieldy. We will study some special cases in order to obtain some insight.

(i) *The most simple case*

Suppose that, except for the fact that predation takes place at prey age $a = 0$, all indices are age-independent. So, in particular,

$$g(a) = \mu e^{-\mu a}$$

$$h(\tau) = f(\tau) = \omega e^{-\omega\tau}.$$

Straightforward manipulations applied to either (2.13) or (3.1) lead to the system of ordinary differential equations

$$(3.6) \qquad \begin{cases} \dfrac{dn}{dt} = \mu\gamma n \exp(-\theta Q\Phi(c)) - \mu n \\[2ex] \dfrac{dQ}{dt} = \zeta\beta^{-1} c\Phi(c)Q - \omega Q \end{cases}$$

with c as a function of n and Q defined by

$$(3.7) \qquad \frac{c\Phi(c)}{\beta} = \mu\gamma\,\frac{n}{Q}\,(1-\exp(-\theta Q\Phi(c)))$$

and

$$n(t) = \int_0^\infty p(t,a)da = \text{total prey population}$$

$$Q(t) = \int_0^\infty \psi(t,\tau)d = \text{total predator population}$$

Of course one can also write down (3.6) directly from the assumptions and the interpretation.

The characteristic equation (3.5) now becomes

$$e\lambda^2 + b\lambda + c = 0 \tag{3.9}$$

where

$$e = 1 + qm(\gamma)$$
$$b = -q\mu(K(\gamma)-m(\gamma)) + \omega m(\gamma)(q-1)$$
$$c = \omega\mu(K(\gamma)-m(\gamma))(1-q).$$

Since $e \geq 0$ and $c \geq 0$ for $\gamma \geq 1$ and $q \in (0,1)$ we conclude that the steady state is stable if $b > 0$ and unstable if $b < 0$. The criticality condition $b = 0$ defines the stability boundary in parameter space. Expressing q as a function of the other parameters we find

$$q(\gamma, \tfrac{\mu}{\omega}) = \frac{-m(\gamma)}{\frac{\mu}{\omega}\ln\gamma - m(\gamma)} = \frac{\ln\gamma-\gamma+1}{\ln\gamma-\gamma+1-\frac{\mu}{\omega}\ln\gamma(\gamma-1)} . \tag{3.10}$$

Some important properties are:

(i) $$\lim_{\gamma\downarrow 1} q(\gamma, \tfrac{\mu}{\omega}) = \frac{1}{2\frac{\mu}{\omega}+1}$$

(ii) $$\lim_{\gamma\to\infty} q(\gamma, \tfrac{\mu}{\omega}) = 0$$

(iii) $$\frac{\partial}{\partial\gamma} q(\gamma, \tfrac{\mu}{\omega}) = \frac{\mu}{\omega} \frac{\ln^2\gamma-(\gamma-1)^2/\gamma}{(\ln\gamma-\gamma+1-\frac{\mu}{\omega}\ln\gamma(\gamma-1))^2} < 0 \quad \text{for } \gamma > 1$$

(iv) $$\frac{\partial}{\partial\frac{\mu}{\omega}} q(\gamma, \tfrac{\mu}{\omega}) < 0 \quad \text{for} \quad \gamma > 1.$$

In figure 2 we display q as a function of γ for various values of $\frac{\mu}{\omega}$. We see that the form of the stability boundary in the (γ,q)-plane is not

influenced by the value of μ/ω.

In the case of a linear functional response (q=0) the steady state is always stable. In fact the corresponding system

$$\begin{aligned} \frac{dn}{dt} &= \mu n(\gamma e^{-\theta Q}-1) \\ \frac{dQ}{dt} &= \zeta n(1-e^{-\theta Q})-\omega Q \end{aligned} \tag{3.11}$$

has a globally asymptotically stable steady state as can be deduced from Bendixson's criterion after the change of variables $n = e^m$, $Q = e^R$.

In Appendix III we modify the system (3.11) to account for the presence of yet another predator species which eats all prey indiscriminately and make a remark about the competitive exclusion principle.

(ii) *prey with small reproductive capacity*

For $\gamma = 1$ the characteristic equation (3.5) has two roots equal to zero. The stability of the non-trivial steady state (3.4) for γ slightly larger than one depends on the sign of the real part of these two critical roots. The procedure to assess the stability properties of the steady-state in such a situation is explained in Appendix I. With this procedure we find that the steady state is stable if and only if

$$(q-1)p+r < 0 \tag{3.12}$$

where $$p = \tilde{f}\,\tilde{\tilde{g}} + \tilde{g}\,\tilde{\tilde{f}} - 2\tilde{g}\,\tilde{h}\,\tilde{f} + 3\,\tilde{g}\,\tilde{f}^2$$

$$r = 2\tilde{g}\,\tilde{f}^2$$

With $$\tilde{g} = \int_0^\infty ag(a)da = \text{the mean of } g(a)$$

$$\tilde{\tilde{g}} = \int_0^\infty (a-\tilde{g})^2 g(a)da = \text{the variance of } g(a)$$

and similar definitions for f and h.

From (3.12) we see that a reduction of the efficiency of the predator (i.e. an increase of q) can cause a stable steady state to become unstable.

In the limit $q \uparrow 1$ the steady state is always unstable.

If we take $\tilde{h} = \tilde{f}$, for instance by putting $K(\tau) \equiv 1$, (3.12) can be written as:

$$(3.13) \qquad q < \frac{-2\tilde{g}\tilde{f}^2}{\tilde{f}\tilde{g}+\tilde{f}\tilde{g}+\tilde{g}\tilde{f}^2} + 1.$$

From (3.13) we see that an increase of the mean age of reproduction of any of the species can destabilize a stable steady state. If we let $\tilde{g} \to \infty$ for fixed $\tilde{f},\tilde{f}$ and $\tilde{g}$ the condition becomes

$$q < 1 - \frac{2\tilde{f}^2}{\tilde{f}+\tilde{f}^2}$$

which still can be satisfied for some positive values of q provided $\tilde{f}$ is sufficiently large (in fact $\tilde{f} >> \tilde{f}^2$). However, if $\tilde{f} \to \infty$ for fixed $\tilde{g},\tilde{g}$ and $\tilde{f}$ we find

$$q < -1$$

which clearly is impossible for positive q. So in this sense the mean age of reproduction of the predator can have a stronger destabilizing influence than the mean age of reproduction of the prey.

(iii) *delayed reproduction and predation*

Next we take the death-rates to be age independent, and the age specific birth rates and the predation index to be step-functions. So,

$$g(a) = H(a-T_1)\mu e^{-\mu(a-T_1)}$$

$$(3.10) \qquad f(\tau) = H(\tau-T_3)\omega e^{-\omega(\tau-T_3)}$$

$$h(\tau) = H(\tau-T_2)\omega e^{-\omega(\tau-T_2)}.$$

With $H(\cdot)$ the Heaviside-stepfunction. T_1 and T_3 are the juvenile period of the prey and predator respectively. T_2 is the pre-predatory period. So, $T_2 \leq T_3$. The stability boundary is determined numerically with a procedure described in Appendix II.

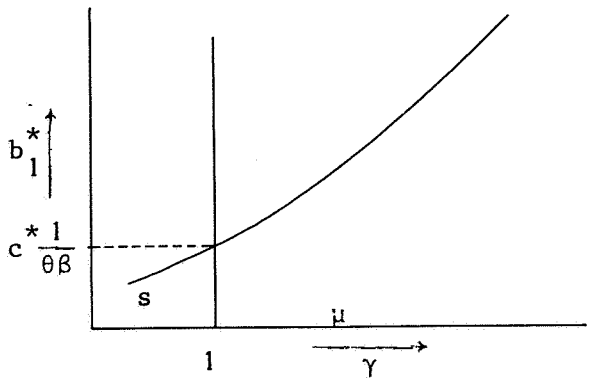

Figure 1: Bifurcation diagram s = stable; μ = unstable.

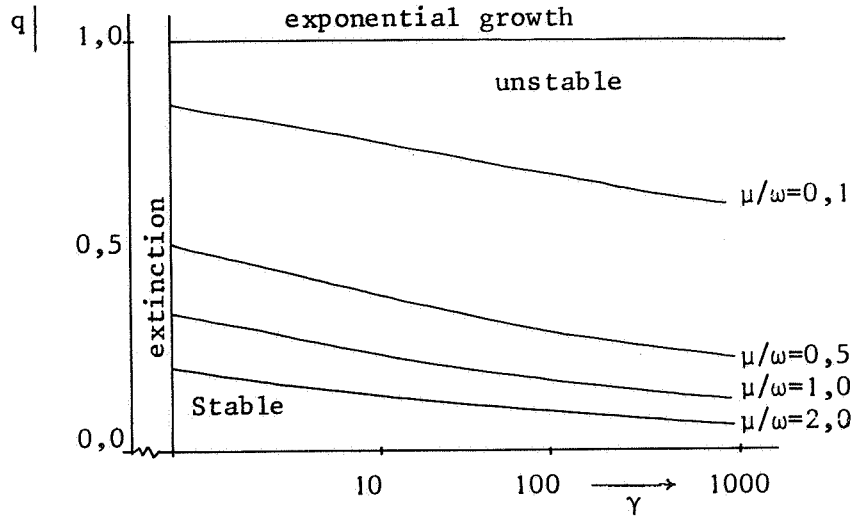

Figure 2: The stability boundary in the (γ,q)-plane of 'the most simple case' for various values of μ/ω.

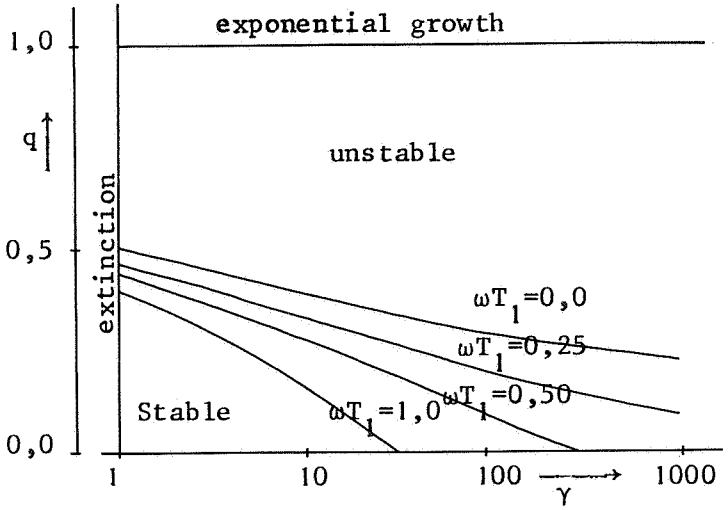

Figure 3: The stability boundary for various values of ωT_1 when $\omega T_2 = \omega T_3 = 0,0$ and $\mu/\omega = 0,5$.

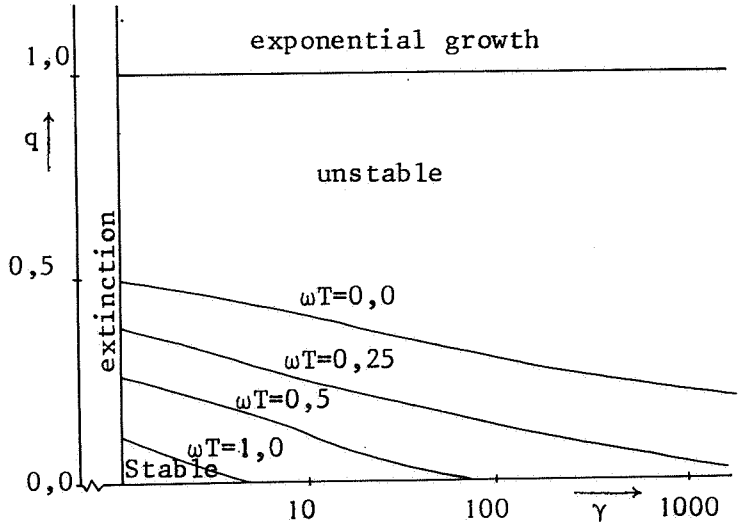

Figure 4: The stability boundary for various values of $\omega T_2 = \omega T_3 = \omega T$ when $\omega T_1 = 0,0$ and $\mu/\omega = 0,5$. For $\omega T > \sqrt{2}$ all non-trivial steady states are unstable.

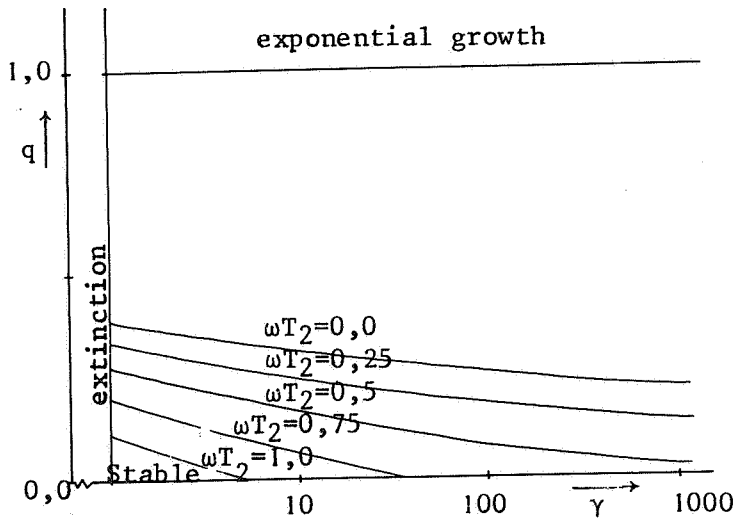

Figure 5: The stability boundary for various values of ωT_2 when $\omega T_1 = 0,0$; $\omega T_3 = 1,0$ and $\mu/\omega = 0,5$.

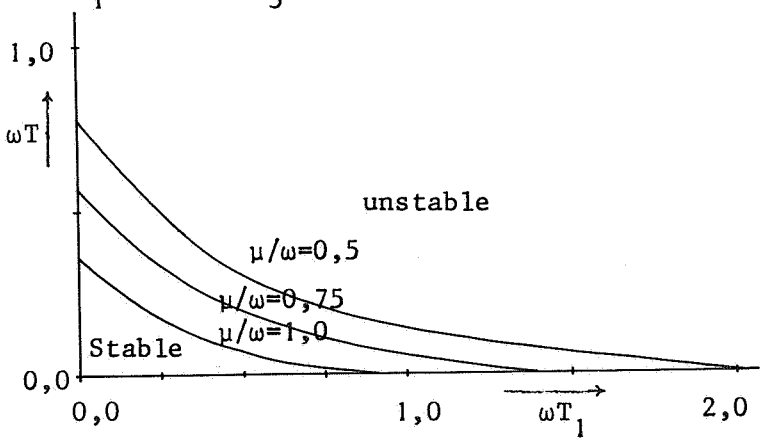

Figure 6: The stability boundary in the $(\omega T_1, \omega T)$-plane, where $\omega T = \omega T_2 = \omega T_3$, for $q = 0,0$; $\gamma = 10,0$ and various values of μ/ω

From figures 3,4 and 5 we see that the form of the stability boundary is not much influenced by variation of the delays in any of the species. The figures shown here are representative for most parameter values we investigated. The general picture is that the stability domain becomes smaller when μ/ω or any of the delays is increased. A comparison of figures 3 and 4 gives the impression that the stability domain is reduced more when the juvenile period of the predator is increased than when the juvenile period of the prey is increased.

When $T_2 \neq T_3$ restabilization can occur when T_3 is increased when μ/ω and ωT_3 are large. This restabilization occurs in a small interval of q values. Although this phenomenon is rather intrigueing, we consider it, in this model, as biologically irrelevant.

In figure 6 we illustrate the destabilizing effect of the juvenile periods in more detail. This figure is representative for all parameter values investigated. From figures 3,4 and 6 we see that the juvenile period of the predator is more critical to the stability of the steady-state than the juvenile period of the prey. We will return to this point in the discussion.

The period P of the periodic solution that arises at the stability boundary seems to depend mainly on γ and not so much on other parameters. We found that P decreases with increasing γ. For $\gamma = 10$ we found $P \approx 10$ for $\gamma = 100$, $P \approx 6$ for $\gamma = 1000$, $P \approx 4$. The time unit in which the period is expressed is 'the mean longevity of the predator' $(1/\omega)$.

4. DISCUSSION

The model we have analyzed in this paper is based on some assumptions that will not be met in the real world. Density dependent effects other than predation are not incorporated in the model. For instance, selfregulation of the prey and/or the predator can be important when the population density is high. These points should be given some attention before we can draw general conclusions about the dynamical consequences of egg-eating predator-prey relations, but some conclusions can already be drawn from the results of section 3.

The well known LOTKA-VOLTERRA model, where prey is eaten

indiscriminately, can be compared with our 'most simple case' with a linear functional response. The LOTKA-VOLTERRA model has a neutrally stable steady-state. The egg-eating predator model has a globally stable steady-state. So, concentration of the predator on very young prey can be considered as a stabilizing mechanism. With model formulations that are disputable (see section 1) GURTIN and LEVINE (1979) concluded that egg-eating is destabilizing while THOMPSON et al. (1982) concluded that it is stabilizing.

The functional response, expressed here through the efficiency factor q, is seen to act as a destabilizing mechanism. It has a major influence on the stability of the non-trivial steady-state. When the predator is very inefficient the steady-state is always unstable. COLEMAN & FRAUENTHAL (1983) also investigated an egg-eating predator model where the predator has a non-linear functional response. They arrived at the opposite conclusion, but, as argued in section 1, their model formulation is disputable.

Delays in reproduction and predation are also seen to be destabilizing. A striking feature of our results is that the range of juvenile periods for which the steady-state is stable is larger in the prey than in the predator species. HASTINGS (1984) analyzed a model where adult prey individuals are eaten by adult predators. In that model the juvenile period of the prey proved to be more critical than the juvenile period of the predator. Furthermore, he found that when the juvenile period of the prey is smaller or equal to that of the predator the steady-state is always unstable. These conclusions differ from the ones derived in the present paper and might point to a qualitative difference between predation on adults and predation on very young individuals.

In conclusion we can say that concentration of the predator on very young individuals is stabilizing, a non-linear functional response and delays in reproduction and predation are destabilizing. The conflicting effects of these mechanisms determine the precise location of the stability boundary.

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APPENDIX I

To assess the stability of the non-trivial steady-state for γ slightly larger than one put $\gamma = 1+\varepsilon$ and consider the characteristic equation as a function F of λ and ε. The expansion of $F(\lambda,\varepsilon)$ about $\lambda = \varepsilon = 0$ is given by

$$F(\lambda,\varepsilon) = A\varepsilon + B\lambda^2 + C\varepsilon\lambda + D\lambda^3 + \ldots$$

since $(\frac{\partial F}{\partial \lambda})_{\lambda=0;\varepsilon=0} = 0$.
Assume that λ can be expanded in powers of $\sqrt{\varepsilon}$, i.e.

$$\lambda = c_1\sqrt{\varepsilon} + c_2\varepsilon + \ldots .$$

Substituting this into the expansion for F we find after equalizing like powers of $\sqrt{\varepsilon}$:

$$c_1 = \pm\sqrt{-\frac{A}{B}}$$

$$c_2 = \frac{AD-BC}{2B^2} .$$

We conclude that:

(i) the steady state is stable if

$$\frac{A}{B} > 0 \quad \text{and} \quad AD-BC < 0$$

(ii) the steady state is unstable if

$$\frac{A}{B} < 0 \quad \text{or} \quad \frac{A}{B} > 0 \quad \text{and} \quad AD-BC > 0.$$

APPENDIX II

We want to find solutions of $F(\lambda,\alpha,\beta) = 0$ where λ is purely imaginary and α and β are real. Assume that F is linear in α. Then the equation can be written as:

$$F(\lambda,\alpha,\beta) = F_1(\lambda,\beta) - \alpha F_2(\lambda,\beta) = 0$$

or

$$\alpha = \frac{F_1(\lambda,\beta)}{F_2(\lambda,\beta)} .$$

Since α is real we necessarily should have

$$\mathrm{Re}F_1\mathrm{Im}F_2 + \mathrm{Re}F_2\mathrm{Im}F_1 = 0.$$

This is an equation in two variables λ and β. For fixed β successive roots λ can be found with standard numerical procedures. Subsequently α can be found from

$$\alpha = -\frac{\mathrm{Re}F_1}{\mathrm{Im}F_2}$$

if $\mathrm{Im}F_2 \neq 0$ and

$$\alpha = \frac{\mathrm{Im}F_1}{\mathrm{Re}F_2}$$

otherwise. Thus we construct curves in the (α,β)-plane on which the equation $F = 0$ has a purely imaginary root. The "outer" one is the true stability boundary. The clue to this method is the first step in which the equation is "solved" for α. When studying (3.5) with f,g and h given by (3.10) we first gave q the role of α and γ the role of β. But when making figure 6 we used a preparatory log-transformation to make the equation linear in ωT and then gave ωT the role of α and ωT_1 the role of β.

APPENDIX III

Assuming linear functional responses, we may describe (after scaling all variables), the interaction of one prey (n), one egg-eating predator (Q) and one indiscriminate eating predator (R) by the system

$$\frac{dn}{dt} = n(\gamma e^{-Q} - 1 - R)$$

$$\frac{dQ}{dt} = Q(nf(Q) - \omega)$$

$$\frac{dR}{dt} = R(\varepsilon n - \zeta)$$

where $f(Q) = \frac{1-e^{-Q}}{Q}$ (so f is monotone decreasing) and $\gamma, \omega, \varepsilon$ and ζ are positive parameters. In the invariant n-R plane we have VOLTERRA-LOTKA dynamics: periodic orbits around the equilibrium $\tilde{n} = \zeta/\varepsilon$, $\tilde{R} = \gamma - 1$. In the invariant n-Q plane there is a globally stable equilibrium $\bar{Q} = \ln\gamma, \bar{n} = \omega \frac{\gamma \ln\gamma}{\gamma - 1}$. The coexistence equilibrium

$$n^* = \zeta/\varepsilon, \quad Q^* = f^{-1}(\frac{\varepsilon\nu}{\zeta}), \quad R^* = \gamma e^{-Q^*} - 1$$

is biologically relevant (i.e., lies in the positive octhant) provided that

$$(*) \qquad \frac{\gamma - 1}{\gamma \ln\gamma} < \frac{\varepsilon\nu}{\zeta} < 1.$$

Under the condition (*) both the $(\tilde{n},0,\tilde{R})$ and the $(\bar{n},\bar{Q},0)$ equilibrium are unstable with respect to the three dimensional system. Some further calculations show that the * equilibrium can not change its stability type while moving (as parameters are varied) from the $(\tilde{n},0,\tilde{R})$ equilibrium to the $(\bar{n},\bar{Q},0)$ equilibrium or vice versa and, moreover, that it is locally asymptotically stable near the bifurcation points. So we conclude that both predators can coexist in a stable steady state if (*) is satisfied, although there is only one food source. They manage to do so by specializing on different stages of the prey. This point was put forward by HAIGH and MAYNARD SMITH (1972) in the context of a slightly more complicated model.

From a mathematical point of view it seems interesting to add saturating functional responses and carrying capacities and to study, in the spirit of WALTMAN (1983), the movement of limit cycles from one invariant plane to another as parameters are varied.

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