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SMR/99-32

AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(16 November - 10 December 1982)

AGE DEPENDENT PREDATION IS NOT A SIMPLE PROCESS

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Age dependent predation is not a simple process.

I. Continuous time models

by

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916-752-7543
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running head: Age dependent predation

Abstract.

The stability of models of age dependent predation in continuous time with predators exhibiting a functional response are analyzed. A number of new features of biological importance emerge that are not present in simpler models. These include limits to the length of juvenile periods (both upper and lower) for stability, and the possibility that increases or decreases in any of the model parameters can be stabilizing or destabilizing. Hence, increased delays are not necessarily destabilizing.
The variance in the length of the juvenile period is shown to be an important factor determining stability. Additionally, the relative stability of predation only on juveniles or only on adults is compared.

INTRODUCTION

The study of predator prey systems began with the early work of Lotka and Volterra, who treated the simplest cases. In recent years, to understand better the dynamical behavior of predator prey systems various complications have been included (see for example the review, Murdoch and Oaten, 1975). One complication that is certainly present is that predators do not eat all ages or sizes of prey indiscriminately. Numerous examples ranging from molluscs to insects to fish illustrate this point.

Some of the best documented cases of age dependent predation are from fish. Nielsen (1980) discusses the interaction between walleye and yellow perch, where the major diet item for adult walleye is juvenile yellow perch (see also Le Cren et. al. 1977 and references in these papers). Paine (1965) discusses how there is a maximum size to prey consumed by *Navanax inermis*, an opisthobranch. Dayton (1971) discusses how *Balanus cariosus* and *Mytilus californianus* escape predation by *Thais* by growing to a large enough size. Many insects are preyed upon only as adults. A spectactular example of this is the periodical cicada (Lloyd and Dybas, 1966). Age dependent predation is also important in cases where the prey is an ungulate, as in the interaction between moose and wolves on Isle Royale (Jordan et. al., 1971). A simple model for this case was analyzed by Gazis et. al. (1973).

Predation only on juveniles or only on adults has been

treated in a number of continuous time models in addition to those mentioned above. For the simple interaction terms used by Lotka and Volterra, predation on only juveniles or only on adults has been shown to act as a stabilizing influence. In fact, the model, which is originally neutrally stable, becomes stable for all values of the prameters (May, 1974 and Smith and Mead, 1974). Similar results obtain for the studies mentioned earlier. Another model, where the predator eats only "eggs", seems to indicate that age dependent predation cannot be stabilizing, and in fact may be destabilizing (Gurtin and Levine, 1979).

In fact, age dependent predation has been extensively discussed in the context of 'prudent predation' (Slobodkin, 1974). This discussion centered on the evolution of prudent predation, partly as a means of leading to stable predator prey systems. Missing was a detailed account of the stability properties of dynamical models with age dependent predation. A particular set of models was analyzed by Maynard Smith and Slatkin (1973).

In the current paper, I will study age dependent predation in continuous time models, but also include an arbitrary functional response by the predator. Since many if not most reasonable functional responses are destabilizng (Murdoch and Oaten, 1975), the question whether age dependent predation can overcome the destabilizing effect and lead to a model with a stable equilibrium is important. The answers turn out to be more complex and interesting than at first supposed. In a following paper I will concentrate on the analogous problem in discrete time models.

More specific questions than whether age dependent predation is stabilizing are also important. One question is whether predation only on juveniles or only on adults is in some sense more stabilizing. Another question is whether the models always become more stable as the proportion of the population at risk declines (or the proportion safe from predation increases). Other questions will arise in the course of the analysis.

THE MODELS

The form of the investigation here will be to examine a series of models and compare the outcomes from each. A single truly general model would be extremely complex, so I resort to considering a number of specific models. The results will be presented in the following section, with all calculations postponed to the appendix.

I will first describe the set of models for the case where predation is only on adults. Let H(t) denote the number of adult prey at time t, and let P(t) denote the number of predators at time t. In the absence of predation, the prey will be assumed to obey the following linear equation, which allows for a juvenile period:

$$(1) \qquad dH/dt = r\int_0^\infty H(t-s)G(\text{[illegible]}s)\,ds \quad - \quad DH,$$

where G(z) is the probability that an individual survives to age z and matures from juvenile to adult at age z and D is the death rate of adults.

If there is a predator with a functional response, the

$$(2) \qquad dH/dt = r\int_0^\infty H(t-s)G(\text{[illegible]}s)\,ds \quad - \quad DH - Pf(H)$$

where f(H) is the functional response of predators to prey (see e.g. Murdoch and Oaten, 1975).

The predator population will obey the following equation:

$$(3) \qquad dP/dt = cPf(H) - kP,$$

where c represents the conversion rate of prey deaths into predator births and k is the death rate for the predator population.

The specification of the model will be complete once the maturity function G(t-s) and the functional response f(H) are specified. I will leave the functional response general, since only its derivative enters into the determination of stability. In fact, for the qualitative results herewhat is most important is whether the response is stabilizing or destabilizing as in the work of Murdoch and Oaten (1975).

For the function G(z) one must be more specific. I will choose several specific forms, including those distributions which allow one to convert the problem to an equivalent one with extra ordinary differential equations (McDonald, 1978). I will concentrate on two extreme cases, namely those leading to the following two models, which are special cases of the model described by equations (2) and (3). The cases correspond to two forms for G(z) that give no variance in the length of the juvenile period or very large variance. The amount of variance in the juvenile period will be extremely important in the behavior of the models.

The models can be more easily understood by direct derivation, however. The first one says that the prey has a juvenile period of fixed length T. Only adults are subject to predation, and only adults can reproduce. This leads to the following model:

(4a) $dH/dt = rH(t-T) - DH - Pf(H)$

(4b) $dP/dt = cPf(H) - kP$

The other possibility that I will consider in detail is the case where there is a maturity rate from juvenile to adult, instead of a fixed period. This leads to the following model:

(5a) $dH_0/dt = rH_1 - d_0H_0 - aH_0$

(5b) $dH_1/dt = aH_0 - d_1H_1 - Pf(H_1)$

(5c) $dP/dt = cPf(H_1) - kP.$

The variables H_0 and H_1 are the sizes of the juvenile prey population and the adult prey population respectively. The new symbols d_0 and d_1 represent predator independent death rates of juveniles and adults respectively. The maturity rate is a, which determines the mean length of the juvenile period.

As a link between the two models above, I will also briefly consider the following model, in which there are two juvenile stages. In fact, the model with a fixed juvenile period can be thought of as one with an infinite number of juvenile stages (McDonald, 1978). The model with two stages is:

(6a) $dH_0/dt = rH_2 - d_0H_0 - aH_0$

(6b) $dH_1/dt = aH_0 - d_1H_1 - aH_1$

(6c) $dH_2/dt = aH_1 - d_2H_2 - Pf(H_2)$

(6d) $dP/dt = cPf(H_2) - kP.$

The meaning of the new symbols is analogous to the uses in the previous models, where H_2 is now the (size of the) adult stage.

Before proceeding to the models which include predation only on juveniles, I will introduce the following model, which is the analog of model (5) with one juvenile stage, but allowing predation on all stages. This serves as a comparison for the stabilizng influence of age depednent predation. The model is:

(7a) $dH_0/dt = rH_1 - d_0H_0 - aH_0 - Pf(H_0 + H_1)H_0/(H_0 + H_1)$

(7b) $dH_1/dt = aH_0 - d_1H_1 - Pf(H_0 + H_1)H_1/(H_0 + H_1)$

(7c) $dP/dt = cPf(H_0 + H_1) - kP.$

Predation only on juveniles

The first model with predation only on juveniles that I will describe is the analog of model (4), with a fixed juvenile period. Let $h_j(a,t)$ be a density function on age a, at time t, for the number of juvenile prey. Let T be the length of the juvenile period. Then the total number of juveniles is

(8) $$H_j(t) = \int_0^T h_j(a,t)\,da.$$

Let $H_a(t)$ be the number of adult prey at time t. Then the adult prey population will obey the equation

(9) $dH_a/dt = h_j(a,T) - d\,H_a.$

where d is the death rate of adults. The juvenile population will obey a vonFoerster type equation, namely:

$$(10)\quad \frac{\partial h_j}{\partial t} + \frac{\partial h_j}{\partial a} = -f(H_j)P,$$

where the only cause of death in juveniles is predation. Additionally, (10) has a boundary condition representing births, namely:

$$(11)\quad h_j(0,t) = bH_a.$$

The predator population will obey the equation

$$(12)\quad dP/dt = PH_j - kP.$$

The model can be simplified somewhat by solving the partial differential equation (10), using the boundary condition (11), assuming $f(H_j)=H_j$ and substituting in (9) and (12), yielding:

$$(13a)\quad dH_a/dt = bH_a(t-T)\exp\{-\int_0^T P(t-s)ds\} - dH_a$$

$$(13b)\quad dP/dt = P\int_0^T bH_a(t-a)\exp\{-\int_0^a P(t-s)ds\}\,da \quad -kP$$

Unfortunately, the model represented by (13) is still quite unwieldy, and will not be analyzed here. Clues to its almost certain curious behavior are to be found below, however.

I will now develop models to illustrate the effects of predation only on juveniles that can be analyzed, at least in part. These are the analogs of models (5) and (6) with juvenile stages. Hence, consider the following two models:

$$(14a)\quad dH_0/dt = rH_1 - d_0H_0 - aH_0 - Pf(H_0)$$

$$(14b)\quad dH_1/dt = aH_0 - d_1H_1$$

$$(14c)\quad dP/dt = cPf(H_0) - kP.$$

The appropriate analog to model (6), is the following where predation includes both juveniles stages, since it is the extension of this model that would evnetually lead to the model embodied in (12) and (13). Hence, consider the following model:

$$(15a)\quad dH_0/dt = rH_2 - d_0H_0 - aH_0 - Pf_0^*(H_0)$$

$$(15b)\quad dH_1/dt = aH_0 - d_1H_1 - aH_1 - Pf_1^*(H_1)$$

$$(15c)\quad dH_2/dt = aH_1 - d_2H_2$$

$$(15d)\quad dP/dt = cPf(H_0 + H_1) - kP.$$

where

$$(16)\quad f_i^*(H_i) = f(H_0 + H_1)H_i / (H_0 + H_1).$$

Although this model will prove too difficult to analyze in great detail, some of its exciting behavior will become apparent in special cases.

RESULTS

The results are in the form of a stability analysis of the unique nontrivial equilibrium point for all the models (when the equilibrium exists), supplemented by numerical integration. All calculations are postponed to the appendices.

In all the models the condition for the existence of the unique nontrivial equilibrium is the same: that the prey population grows (without bound) in the absence of the predator. This can easily be translated into an appropriate algebraic condition for all of the models. Another feature common to all the models is that the equilibrium level of the prey stage at risk does not depend on the length of the juvenile period. This is a consequence of the assumption of no interference among the predators. Only the equilibrium level of the group not at risk changes as the length of the juvenile period changes. In all cases the equilibrium behavior is simpler when the prey class at risk from predation has no other source of mortality. In this case the survival of the prey in the absence of the predator is independent of the length of the juvenile period.

The model (4) with a fixed juvenile period has the following behavior, as can be shown using recent results of Cooke and Grossman (1982). If the functional response is stabilizing, then the equilibrium is stable for all values of all the parameters when it exists. It is for the destabilizing functional response that the curious behavior is present. Then when the juvenile period T=0, the nontrivial equilibrium is unstable. As T increases the equilibrium may become stable, then unstable, stable, etc, with any number of switches possible. (This is illustrated for some examples in Table 1). For sufficiently large values of T the equilibrium is unstable. The results can be understood as an interplay between a resonance effect and the destabilizing effect of time delays. The time

delays for which the model is unstable represent the length of the predator prey oscillation (see table 1). Hence the first set of switches is biologically most meaningful. *Note that depending on the length of the juvenile period, either an increase or a decrease in the juvenile period can be either stabilizing or destabilizing.*

Another consequence of the switching behavior is apparent from table 1. *Either an increase or a decrease in the other parameters of the model, namely the birth rate b, and adult death rate d, can be either stabilizing or destabilizing.* In a similar fashion either an increase or a decrease in the death rate of the predator can be stabilizing or destabilizing.

For almost all parameter values except those with very large values of r/k (prey birth rate to predator death rate) or extremely destabilizing functional responses there is at least one interval of stability (in terms of the length of the juvenile period.) Multiple switches require small values of r/k or only slightly destabilizing functional responses. Here small values of r/k are those in the range 0 to to .1, which would represent very long lived prey. Large values would be greater than 10 representing very short lived prey. A very destabilizing functional response would have a slope significantly less than half that of the Lotka-Volterra (linear) response at the equilibrium.

Numerical integration of this model indicates that the trajectories get very close to the axes for those parameter values for which the equilibrium is unstable. Hence, the stability of the equilibrium point here may be a good indication of the possibility for persistence of the system.

The behavior of the model with a single juvenile period is simple by comparison. Only one switch from instability to stability is possible. If the functional response is stabilizing stable for all parameter values. If the functional response is destabilizing, then stable if and only if the maturation rate is slow enough.

Not surprisingly, the model with two juvenile stages is already complex enough to allow several switches. This is expected, since the model (4) can be represented as one with an infinite number of juvenile stages. The variance in the juvenile period is already small enough in this case for the resonance effect to occur.

The stability of the equilibrium of the model (7) with two prey stages and age independent predation provides a standard. Here stability is determined solely by whether the functional response is stablizing or destabilizing.

The behavior of the models with predation only on juveniles is of similar complexity, but with some important differences. I wll first consider the model with one juvenile stage. Again, if the functional response is stabilizing, the model is stable independent of the length of the juvenile period. However, if the functional response is destabilizing there are two possibilities. The first is that the model has a stable nontrivial equilibrium only if the juvenile period is short enough. The other possibility occurs when the functional response is extremely destabilizing. Then, the model is unstable

no matter how short the juvenile period is. The reason for this difference will be discussed below.

The model with predation on juveniles with two stages, which represents a reproduction in the variance in the length of the juvenile period, already has very complex behavior. This is apparent even when the functional response is of the simplest form, namely the linear Lotka-Volterra response. Even this model is too complex to study in detail, so I will discuss several particular cases illustrating the possibilities. First assume that the only cause of death in the juvenile stages is predation, so $d_0=d_1=0$. Next, assume (possibility after suitable normalizations, see appendix) that $c=k=1$. Finally, in both cases the death rate of the adult prey will be small, with $d_2=0.1$/ (1) Then, if $r=1$, the model is stable only if the juvenile stages are short enough. (2) However, if $r=3.5$, the model is stable only if the juvenile stages are neither too short nor too long. In particular the necessary and sufficient condition for stability is approximately:

(17) $.005 < a < .02.$

(3) Still more complicated behavior is possible. If $r=2.5$, then the equilibrium is stable if the juvenile period is extremely short, or of intermediate length, with a region of instability in between. The necessary and sufficient condition for stability is approximately:

(18a) $0.291 < a$,

or

(18b) $0.006 < a < 0.061$.

Two other possible behaviors are clearly possible in models with more complex functional responses, namely stability for all lengths of juvenile period, or instability for all lengths of juvenile period.

This last example illustrates another way in which predation only on juveniles is less stable than predation only on adults. With predation only on adults, and a linear (Lotka-Volterra) functional response the model is stable. With predation only on juveniles, and a linear functional response, the nontrivial equilibrium can be either stable or unstable, depending on the parameters. This confirms in part the results of Gurtin and Levine (1979) for a very different model, but suggests a more complex situation. In their model, predation only on eggs always destabilized a Lotka-Volterra model. For the model here, the results are dependent on the length of the juvenile period and the other parameters of the model.

DISCUSSION

Here I will provide heuristic explanations and biological implications for the results here. I will begin with a general discussion of the destabilizing role of delays, and then continue with some of the more specific results in this paper.

The ecological literature has often contained statements to the effect that time delays are destabilzing. The models in this paper do not illustrate this. I should first note that McDonald (1976) discussed the possibility of at least a single switch from stability to instability to stability for a predator prey model with 'lag' in the predator response, and that Cushing and Saleem (1982) discussed how a shorter juvenile period could lead to instability in a similar model. Additionally, Cushing (1982) discussed how longer maturation periods might be stabilizing in a model for a single species with age structure consuming a logistically renewing resource. These earlier results combined with those in this paper based in part on the mathematical analysis of Cooke and Grossman (1982) should put to rest once and for all the simple notion that delays are destabilizing. Reality is far more complex. A system can switch between instability and stability several times as a delay is increased. There is a simple heuristic explanation for this complex behavior, namely that there is a resonance interaction between the inherent periodic nature of the predator prey interaction and the length of the delay. This is illustrated by the fact that delays corresponding to multiples of the period of the predator prey system (as determined by linearization) are those that lead to instability. Additionally, the possibility of multiple switches between stability and instability is increased as the variance in the delay is decreased. The phenomenon under discussion may be of great importance in ecological systems, since even competitive systems with more than two species can exhibit oscillations (May and Leonard, 1975), leading to the possibility of similar interactions with lengths of juvenile periods (delays).

The results in this paper indicate a new kind of limit on the length of juvenile periods, namely that imposed by stability considerations. Particularly for the model with a fixed juvenile period and destabilizing functional response, only certain length juvenile periods lead to stability. Predator prey systems with prey having a juvenile period of the 'wrong' length would not be found, as prey and predator would not coexist. Additionally, as indicated above, this restriction on the length of juvenile periods is likely to be present in many multispecies systems as well. Thus the restriction on the length of juvenile period indicated here may prove to be important for many species, providing an explanation independent of physiological or optimization arguements, or discussions based on coevolution (e.g. Wilbur, 1980).

For the model with a fixed juvenile period as well as any other model with a small enough variance in the juvenile period, the dependence of stability on the parameters is quite complex. Here too, generalizations based on the intuition from simpler models is shown to be dangerous. *Increases or decreases in any of the parameters in the model can be either stabilizing or destabilizing.* This provides an easy explanation for a wide variety of potential behaviors of predator prey systems.

The importance of the *variance* in the length of the juvenile period on the stability of the systems analyzed here is one of the few generalizations possible for the models in this paper. At least in some cases, an increase in the variance in the length of the juvenile period has a stabilizing influence. Contrast the behavior of the two models with predation only on adults with a fixed juvenile period and a juvenile period determined by an exponential process. With a fixed juvenile period, the system is unstable if the juvenile period is too long. However, with the large variance in the juvenile period with the exponential process, the system is stable if the juvenile period is long enough. As a possible illustration of this theme, many amphibians have long and extremely variable juvenile periods (Wilbur, 1980). Perhaps, this is a stabilizing influence.

Finally, it is shown here that predation on juveniles only is in several senses less stable than predation on adults only. Why? A heuristic explanation is possible, if the idea of extinction replaces stability. Predator prey systems collapse, in general, when the predator eats all (or almost all) of the prey, and then starves. If the predator eats juveniles only, a steady supply of food will be present until the adults die off, leading to the collapse of the system. If the predator eats only adults, however, and the juvenile period of the prey is not short compared to the mean lifetime of the predator, then the predator cannot (virtually) eliminate the prey. Thus the system does not collapse. The effect described in this paragraph is more important than any destabilizing effect of delay, at least when the variance in the length of the juvenile period of the prey is large.

The results in this paper indicate some of the myriad complexities possible with age dependent predation. For all of the natural systems mentioned in the introduction, the dynamical behavior and in particular the dependence on the various parameters describing the interaction will almost certainly be complex. Much further work needs to be done. One additional facet of this problem will be discussed in a future paper that will consider discrete time versions of the models discussed here, which will allow a more complete discussion of predation only on juveniles. Other, more complex models are currently under study.

APPENDIX

I will discuss the stability analysis of model (4) in detail. I will outline the stability analysis for the other models, as the techniques are standard and the algebra complex.

The stability analysis of (4) follows the analysis of Cooke and Grossman (1982), who analyzed the stability properties (presence of roots λ with positive real part) of the following equation:

$$A\lambda + B\lambda \exp(-\lambda t) + C = 0, \tag{A1}$$

which is a special case of equation (12) in their paper. As a first step in the analysis of the model (4) I will scale time and H to eliminate c and k. After appropriate redefinitions of the

parameters and the functional response f, the model (4) becomes (where all the parameters have been rescaled):

$$dH/dt = rH(t-T) - DH - Pf(H) \tag{A2a}$$

$$dP/dt = Pf(H) - P. \tag{A2b}$$

This has at most a single nontrivial equilibrium point:

$$\hat{H} = f^{-1}(1) \tag{A3a}$$

$$\hat{P} = (r-D)\hat{H}. \tag{A3b}$$

Linearization of (A2) about the equilibrium (A3) yields

$$dh/dt = rh(t-T) - Dh - p - \hat{P}f'(\hat{H})h \tag{A4a}$$

$$dp/dt = \hat{P}f'(\hat{H})h. \tag{A4b}$$

Here h and p represent deviations from the equilibrium values of H and P, respectivwly. Substitute solutions of the form of a constant times exp(λt) for p and h, and find admissible lambda's to determine the (local asymptotic) stability of the equilibrium. If all solutions lambda have negative real part, then the solution is stable, if there is a lambda with positive real part, then the solution is unstable. (For a mathematical discussion of all this, see El'sgol'ts and Norkin, 1973).

The manipulations indicated above show that lambda satisfies an equation of the form (A1) where:

(A5a) $A = D + (r-D)q$

(A5b) $B = -r$

(A5c) $C = (r-D)q$

and q is defined as

(A6) $q = \hat{H}f'(\hat{H})$.

Following Cooke and Grossman (1982) define w^+ and w^- as the larger and smaller roots of:

(A7) $w^4 + (A^2 - B^2 - 2C)w^2 + C^2 = 0$.

Then define the two sequences

(A8a) $\tau_{n,1} = (\cos^{-1}(-A/B) + 2\pi n)/w^+$

(A8b) $\tau_{n,2} = (\cos^{-1}(-A/B) + 2\pi n)/w^-$,

where $\cos^{-1}$ is evaluated for an angle between π and 2π in (A8a), and for an angle between 0 and π in (A8b). (This condition is not indicated at this point in Cooke and Grossman, but is indicated in their earlier example.) Finally, note that the mdoel is unstable for T = 0 if the functional response is destabilizing (sensu Murdoch and Oaten, 1975). If the functional response is stabilizing, the model is table for all T. If the functional response is destabilizing, then the model is stable

for values of T that satisfy

(A9) $\tau_{k,2} < T < \tau_{k,\text{[illegible]}}$.

Cooke and Grossman (1982) show that the inequality

(A10) $\tau_{k,2} < \tau_{k,\text{[illegible]}}$,

is either valid for no values of k, or for all $k \leq K$ where K is a finite integer (and no other values of k). The results reported in Table 1 of the text are obtained by a numerical computation of the condition (A9).

The analysis of all the other models in the paper is quite straightforward. In all cases the model is linearized about the nontrivial equilibrium point. The stability of the equilibrium is examined by applying the Routh-Hurwitz criteria (pg. 1119 in Gradshteyn and Ryzhik, 1980) to the chracteristic equation of the Jacobian matrix that determines the linearization. In every case, the critical (stability determining condition) turns out to be the one that corresponds to having an eigenvalue on the imaginary axis. It is this condition which is discussed explicitly with refernce to model (15). I will not discuss the very messy algebraic details.

As an illustration of the techniques, I will discuss the scaling used to analyze the model (14) and the resulting stability conditions. The first step is to change the model to one where $d_0 = 0$. This is accomplished by defining

(A11) $a^{*} = a + d_0$

and

(A12) $H_0^{*} = (1 - d_0/a^{*})H_0$.

Then by rescaling time and the variable P, suitably redefining f, and the other 'rescaled' parameters, one arrives at a model of the form (14), but with $d_0=0$ and $c=k=1$. This simplifies the algebra considerably. Finally, note that if only *a* is allowed to vary, the quantity Pf', at equilibrium, is a constant times *a*. Hence, define:

(A13) $z=Pf'/a$.

Then the appropriate Routh-Hurwitz criteria for stability are all always satisfied except the one corresponding to a root crossing the imaginary axis, which becomes:

(A14) $a^2(z+d+2zd-r+z^2+z^2d-zr) + a(d^2 + zd^2 -rz) > 0$.

Hence, there are three cases. If

(A15) $d(1+z) > r$

(A14) is satisfied for all a. If

(A16) $d(1+z) + z > r > d(1+z)$

then (A14) is satisfied only for sufficeintly large a. If

(A17) $r > d(1+z) + z$,

then (A14) is satified for no positive values of a. Using the equilibrium value of P to interpret these conditions in light of stabilizing versus destabilizing functional responses, one obtains the results reported in the text.

Other cases discussed in the text are similar.

Acknowledgement. I thank Ken Cooke for helpful discussions and showing me his paper prior to publication. I also thank Jim Cushing for sending me his work. Discussions with John Gillespie and Elaine Fingerett also helped. Supported in part by NSF DEB 8002593.

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Table 1. Stability results for the model (4) with a fixed juvenile period and predation only on adults. The equilibrium point is stable only for T values (juvenile periods) lying between $\tau_{n,2}$ and $\tau_{n,1}$, as given below. The last column is multiples of the period of the predator prey oscillation with no juvenile period, as determined by linearization.

r	D	q	n	$\tau_{n,2}$	$\tau_{n,1}$	(n+1)period
0.04	0.02	0.8	0	3.82	43.04	49.68
			1	57.03	89.41	99.36
			2	110.25	135.77	149.04
			3	163.46	182.14	198.72
			4	216.68	228.51	248.40
			5	269.89	274.88	298.08
0.2	0.1	0.8	0	1.86	17.69	22.23
			1	27.76	36.74	44.46
			2	53.66	55.79	66.68
2.0	1.0	0.8	0	0.81	4.08	7.07
10.0	6.0	0.8	0	0.58	1.27	3.60
0.4	0.1	0.5	0	3.43	9.39	16.54