

LETTER TO THE EDITOR

**Competition Between Age Classes, and the Stability of
Stage-structured Populations: A Re-examination of
Ebenman's Model**

Traditional models of population growth do not take account of interactions between age classes. The outcome of such interactions is crucial to comprehend the emergence and evolution of complex life cycles (Wilbur, 1980), i.e. of life cycles that involve passage through two or more ecologically distinct stages, as in holometabolous insects. One of the most obvious advantages that complex life cycles may bring is the reduction of competition between stages through habitat or niche differentiation. But it is not yet clear whether such cycles are stable or unstable over ecological and evolutionary time (see a review in Wilbur, 1980).

May *et al.* (1974) and Tschumy (1982) investigated the behaviour of a general discrete model with two age classes, and concluded that competition between age classes is generally destabilizing. Recently, Ebenman (1987, 1988) introduced a competition coefficient explicitly in the model, and showed that increased competition between age classes could in fact be stabilizing. He concluded that this stabilization occurs: (1) when the maximum survival rate from juveniles to adults is high in populations with density-dependent reproduction, or when the maximum birth rate is high in populations with density-dependent survival; and (2) when the density-dependent feedback on reproduction is small compared with that on survival, in populations with reproduction and survival both density-dependent. I shall show that both these conclusions are not generally correct, and that the conditions under which competition between age classes is stabilizing are probably rarely met by natural populations.

Density Dependence in a Single Age Class

The discrete model of Ebenman (1987, 1988) has the general form

$$\begin{aligned}N_0(t+1) &= N_1(t)Bf, \\ N_1(t+1) &= N_0(t)Sg,\end{aligned}\tag{1}$$

where N_0 and N_1 are the densities of juveniles and adults respectively, B is the maximum per capita birth rate and S is the maximum survival rate from juveniles to adults. The functions f and g express the density dependence of birth and survival

rates respectively. They are such that:

$$\begin{aligned} f &= f[N_1(t) + \alpha N_0(t)] \quad \text{and} \quad g = g[N_0(t) + \beta N_1(t)]; \\ f' &= \partial f / \partial N_1 \leq 0 \quad \text{and} \quad \partial f / \partial N_0 = \alpha f' \leq 0; \\ g' &= \partial g / \partial N_0 \leq 0 \quad \text{and} \quad \partial g / \partial N_1 = \beta g' \leq 0; \end{aligned}$$

where α and β are between-age-class competition coefficients.

It is in general impossible to obtain analytical solutions for the equilibrium densities N_0^* and N_1^* , which can be multiple. Therefore Ebenman only analysed the special cases where either reproduction only or survival only is density-dependent. Since the model is symmetric, the analysis of the two cases is identical. Let us consider the first case, with $g = 1$. Ebenman showed that in this case the unique equilibrium point is locally stable if

$$\alpha < S \quad (2)$$

and

$$F = -N_1^* S B f' < 2. \quad (3)$$

Condition (2) sets an upper bound on α . Because $N_1^* = C / (S + \alpha)$ where C is a constant, as Ebenman showed, $dF/d\alpha < 0$, and condition (3) sets a lower bound on α . Hence Ebenman's claim that increasing α is stabilizing as long as α is smaller than S .

This claim is hasty, however. For increasing α to help fulfilling condition (3), it is further necessary that the lower bound set on α by (3) lie in the biologically feasible region of α , i.e. $\alpha \geq 0$. In the limiting case $\alpha = 0$, system (1) collapses to a single-age-class model (Rodriguez, 1988), which, in the case $g = 1$, reduces to:

$$N_1(t+2) = N_1(t) S B f[N_1(t)]. \quad (4)$$

If this single-age-class model is stable, condition (3) is satisfied for the lowest possible α ($\alpha = 0$), and increasing α will not help to satisfy it.

Let us take an example with a specific function f . Ebenman chose a negative exponential function to illustrate the stabilizing effect of increasing α . With that function, the stability of the single-age-class model (4) depends only on the lumped parameter SB , which is in fact the potential finite rate of increase of the population. Consequently, increasing B will always lead to parameter regions where increasing α is stabilizing. Let us choose instead the more flexible function proposed by Hassell (1975):

$$f = [1 + a(N_1 + \alpha N_0)]^{-b}. \quad (5)$$

The stability condition of system (1) with $g = 1$ is then:

$$S \left\{ \frac{1}{2} b [1 - (SB)^{-1/b}] - 1 \right\} < \alpha < S. \quad (6)$$

(The stability condition printed in Ebenman, 1988, is wrong for this function.) It is easy to check that the condition for the left-hand expression to be positive is precisely that the corresponding single-age-class model is unstable (Hassell, 1975). In particular, for $b \leq 2$, it is always negative, and the first inequality in (6) is always satisfied. Now, Hassell *et al.* (1976) showed that almost all natural populations to

which the corresponding single-age-class model was fitted fall into the region of stability. This means that for almost all natural populations, increasing α should not facilitate fulfillment of condition (3).

It is possible to be more precise. A discrete system is all the more stable as its eigenvalues approach zero (when these are zero, any perturbation from the equilibrium is wiped out in a single generation). The eigenvalues of system (1) with $g = 1$ are

$$\mu = -E \pm \sqrt{E^2 + 1 - F}, \quad (7)$$

where $E = -N_1^* B\alpha f'/2$ and $F = -N_1^* SBf'$ as before.

At $\alpha = 0$, these eigenvalues reduce to $\mu = \pm \sqrt{1 - F}$. Let us consider how they move in the complex plane when α is increased slightly above zero. Recall that $dF/d\alpha < 0$, and note likewise that $dE/d\alpha > 0$.

- (1) If $F \leq 1$, the two eigenvalues are real and symmetrical in relation to zero. Increasing α makes them shift to the left and move apart along the real axis. Thus the negative eigenvalue moves away from zero, and stability is reduced.
- (2) If $F > 1$, the two eigenvalues are imaginary and symmetrical in relation to the real axis. Increasing α makes them move to the left of the imaginary axis and get closer. Their modulus, equal to $F - 1$, decreases, hence stability is increased.

In conclusion, when $F \leq 1$ at $\alpha = 0$, that is, when the corresponding single-age-class model shows monotonic damping of perturbations from the equilibrium, competition between age classes can only destabilize the population. When $1 < F < 2$ at $\alpha = 0$, that is, when the corresponding single-age-class model shows oscillatory damping, a slight amount of competition between age classes can increase the degree of stability of the population. When $F > 2$ at $\alpha = 0$, that is, when the corresponding single-age-class model shows a cyclic or chaotic behaviour, a slight amount of competition between age classes can turn an unstable equilibrium into a stable one. Since most natural populations seem to show monotonic damping of perturbations according to Hassell *et al.* (1976), competition between age classes is probably seldom stabilizing in nature. Of course, this does not detract from the theoretical interest of such a possible stabilizing effect, no more than from that of possible limit cycles and chaos in single-age-class population models, especially in view of the limitations inherent in the approach of Hassell *et al.* (1976), as the latter themselves pointed out.

Adult vs. Juvenile Competition

The general case where both reproduction and survival are density-dependent was investigated by Ebenman (1987) by simulation using specific functions f and g of the negative exponential form ($f = \exp[-k(N_1 + \alpha N_0)]$ and $g = \exp[-k'(N_0 + \beta N_1)]$). Ebenman concluded that competition between age classes has a stabilizing effect when density-dependent feedback on reproduction is small compared with that on survival ($k < k'$), whereas if $k > k'$, it has a destabilizing effect.

From a theoretical viewpoint, these asymmetrical results are surprising given the perfect symmetry of system (1). In fact they rest entirely on the break of symmetry

introduced by the implicit assumptions in the simulations that $B > 1$ and $S < 1$, which were also made by Tschumy (1982). These assumptions in turn rest on the particular units with which population biologists are used to working, that is, numbers or densities of individuals. Indeed, in any persistent population, each adult must on average produce more than one juvenile ($B > 1$), and the number of juveniles can only decrease during their development ($S < 1$). The choice of units is, however, arbitrary. One could just as well choose ecological units of biomass or energy content without altering the behaviour of the model. Using such units, it is obvious that $B < 1$ and $S > 1$ are possible. Many insects, such as mayflies, caddis-flies or butterflies, in which the larva ensures the bulk of nutrition and biomass build-up while the adult feeds little if at all, are examples.

In general, when density dependence is achieved by exploitation competition, the stage that exploits the largest amount of resources and contributes most to biomass build-up will also be the one where the main density dependence occurs, which constitutes a factor of stabilization of populations without competition between age classes. When biomasses are converted into numbers of individuals, k and k' will vary inversely with S and B respectively, hence the ratio k/k' will increase concomitantly with (in effect, as the square root of) the ratio B/S . Thus populations regulated by exploitation competition, even those mainly regulated in the larval stage, will often be able to satisfy Ebenman's qualitative condition framed in numbers of individuals as units that k not be small compared with k' , that is, the condition for competition between age classes to be destabilizing. Again, the conclusion emerges that competition between age classes may be seldom stabilizing in nature.

As the foregoing shows, Ebenman's claim that populations of organisms with relatively intense competition between age classes should be more stable when density dependence is primarily on juvenile survival than when it is primarily on reproduction, while the reverse should be true for organisms with no or weak competition between age classes, is unfounded theoretically. This casts serious doubts on the validity of his discussion of specific examples conforming to his predictions (Ebenman, 1988). As Ebenman himself admits, the data come from different studies and different species, and thus are difficult to compare. Other, much more straightforward interpretations are also possible. As an example, let us examine the case of the weevils *Callosobruchus*, in which adults and larvae do not compete. Ebenman interpreted the greater stability of the populations of *C. chinensis* compared with those of *C. maculatus* in some laboratory experiments as a consequence of the fact that reproduction was density-dependent in the former species but not in the latter, in accordance with his predictions. But the pattern has probably nothing to do with his predictions; it can be readily explained by the simple fact that the first species had two independent regulation processes (one in the larval stage and the other in the adult stage), while the second species had only one (in the larval stage) in those experiments (Bellows, 1982).

In short, the contribution of Ebenman was to point to the theoretical possibility of competition between age classes acting as a stabilizing factor of population dynamics. But he failed to properly analyse the conditions under which this stabiliz-

ation can occur. These conditions are such that competition between age classes should generally be destabilizing in natural populations, as suggested by previous authors (May *et al.*, 1974; Tschumy, 1982). Therefore, all other things being equal, complex life cycles, involving habitat or niche differentiation between stages, should generally be more stable than simple ones.

*Department of Animal Biology,
C.P. 160, Université Libre de Bruxelles,
50 av. Roosevelt, B-1050 Brussels, Belgium*

M. LOREAU

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