POPULATION DYNAMICS IN THE SERIAL TRANSFER SYSTEM: COMMENTS ON HADDON'S MODEL

Haddon (1982) has recently proposed a model of the dynamics of population growth in the presence of competitors. He prefers this model to others previously proposed (Ayala et al. 1973; Gilpin and Ayala 1973) because (1) his model predicts more accurately the observed equilibria and (2) it provides a mechanistic explanation for nonlinear per capita rates of population growth. The purpose of this note is twofold. First we show that Haddon's model is a special case of a more general model of population dynamics in the serial transfer system. Secondly, we point out that Haddon's criteria for preferring one model over another ignore several important factors.

We shall concentrate on the single species version of Haddon's model, although our comments apply with equal strength to the two-species competition equations. Haddon's model can be expressed as

$$N_t = sN_{t-1} + f(N_{t-2})[K_J - f(N_{t-2})]/K_J \tag{1a}$$

$$f(N_{t-2}) = N_{t-2} \exp[r(K_A - N_{t-2})/K_A] \tag{1b}$$

in which N_t is the number of adults present at time t; s is the survivorship of adults from one census time to the next; r is the intrinsic rate of increase of the species; K_J and K_A are the carrying capacities of the juveniles and of the adults, respectively. Equation (1a) is a second-order nonlinear difference equation. In Mueller and Ayala (1981) we have shown that when cultures are maintained for 4 wk, then the population dynamics of the serial transfer system can be represented as a fourth-order difference equation:

$$N_t = f_1(N_{t-1}) + f_2(N_{t-2}) + f_3(N_{t-3}) + f_4(N_{t-4}). \tag{2}$$

At any time, the total number of adults censused in the serial transfer system represents contributions from cultures 1, 2, 3, and 4 wk old. The contributions of these four cultures are represented by the various $f_i(N_{t-i})$ functions. It can be seen that the models (1) and (2) are related by

$$sN_{t-1} = f_1(N_{t-1})$$
$$f(N_{t-2})[K_J - f(N_{t-2})]/K_J = f_2(N_{t-2}) + f_3(N_{t-3}) + f_4(N_{t-4}).$$

Adults that emerge from cultures 2, 3, and 4 wk old are added together and described by one function in Haddon's model. Thus model (2) incorporates all the empirical information available with respect to age structure, whereas Haddon's model does not.

We have also shown previously (Mueller and Ayala 1981) how it is possible to derive an asymptotic per capita rate, λ_N, of population growth at a single density. The analysis requires making a linearization of the general model (2) and then obtaining experimental data of the appropriate type in order to estimate the

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constants in the resulting fourth-order linear difference equation. We further went on to show that λ_N is not a linear function of density, as required by the logistic model, and that the deviations from linearity can be well described by the addition of the parameter θ to the logistic equation.

It should be emphasized that our analysis (Mueller and Ayala 1981) has two separate components. The first is the construction of a general model of population dynamics in the serial transfer system. The resulting model (2) explicitly demonstrates that, in general, the adult population size in the serial transfer system is a function of the population size at four previous time intervals. The second part of our analysis shows how one can derive a rate of population growth that is a function of only one density. Using the values thus obtained, we were able to explore some basic assumptions inherent in some simple models of population growth.

Because Haddon's model is only a second-order difference equation, it is clearly not adequate as a general model of population dynamics in the serial transfer system (although it could be appropriate for organisms with two distinct life stages if these are separately sampled). In addition, we must point out that the age structure of *Drosophila* cannot be accounted for in the serial transfer system. Adults are the only life stages censused and, moreover, the adults in the leading culture are of various unknown ages. The age structure (partially) incorporated by Haddon's model is really an age structure of cultures and not of individual flies; i.e., the terms in equation (2) are contributions to the population from variable age cultures, not individuals.

Even though Haddon's model is inappropriate for the serial transfer system, still his comments concerning the theta model deserve attention. Haddon feels that parameters of a model should not only account for empirical observations but also provide mechanistic explanations. The empirical observations have shown that per capita rates of population growth are not linear functions of density (Ayala et al. 1973; Pomerantz et al. 1980; Mueller and Ayala 1981; Hastings et al. 1981). The addition of the parameter θ to the logistic equation seems to account adequately for these deviations from linearity (Mueller and Ayala 1981). It is true that the parameter θ provides no explanation for these deviations; it is merely a device for incorporating this empirical fact in a relatively simple model. Certainly, there can be many phenomena causing these nonlinearities. Schoener (1978) has shown that nonlinearities may result simply from the mechanism of feeding for a limited food supply. Gilpin et al. (1976) have suggested that nonlinearity may arise because quality resources are exhausted first in an environment with heterogeneous resources. These and other phenomena may be in operation for different organisms. The appeal of the theta model is that all such examples might be described adequately by one model. Nevertheless, as we have previously discussed (Mueller and Ayala 1981), uncovering the biological mechanisms responsible for the observations is an important component of understanding population dynamics and deserves further attention.

Levins (1966) has suggested that we try to maximize the generality, precision, and reality of any biological model. It is usually not possible to maximize all three simultaneously (Ayala et al. 1973). Haddon clearly prefers to maximize the reality of a model. This will be done by sacrificing generality and precision. Clearly the

special population structure incorporated by Haddon in model (1) or by us (Mueller and Ayala 1981) in model (2) makes these models less general than either the logistic or the theta models. We submit that when precision is properly defined, the more complicated models suffer with respect to this criterion also. As we have previously discussed (Mueller and Ayala 1981), more complicated models of population growth will almost always yield predicted rates of population growth (and equilibrium population sizes) that are closer to the observed values, simply because they use more parameters. As an extreme case, if $n+1$ distinct observations are made, one can always construct an nth-order polynomial that passes through all the observations. More complicated models, however, are liable to have a much higher mean squared error of prediction. For this reason, an appropriate criterion for identifying the most precise model is to select that which minimizes the mean squared error of prediction (see Mueller and Ayala 1981 for details). Accordingly, Haddon's observation that his model yields a more accurate prediction of the two-species equilibrium is not evidence that his model is more precise in any meaningful way.

We agree with Haddon's desire to understand the mechanisms responsible for deviations from the logistic model. However we do not think that the explicit incorporation of the mechanisms in models of population growth is either necessary or, in some cases, desirable.

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