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https://escholarship.org/uc/item/6sc7r8rd

Journal

Theoretical Population Biology, 9(1)

ISSN

0040-5809

Authors

Gilpin, Michael E
Ayala, Francisco J

Publication Date

1976-02-01

DOI

10.1016/0040-5809(76)90031-9

Copyright Information

Peer reviewed

Schoener's Model and *Drosophila* Competition

Michael E. Gilpin

Department of Biology, University of California at San Diego, La Jolla, California 92037

AND

Francisco J. Ayala

Department of Genetics, University of California at Davis, Davis, California 95616

Schoener (1973) has recently discussed a simple model of growth and competition. It is one that we did not include in the list of models we (Ayala, Gilpin and Ehrenfeld, 1973; Gilpin and Ayala, 1973), fitted to data on interspecies competition between *Drosophila willistoni* and *D. pseudoobscura*. Since we were striving there for completeness, we should like in this note to treat Schoener's model in the spirit of our earlier work. Schoener's single-species growth model is:

$$dN/dt = rN[(I/N) - C - bN].\qquad(1)$$

I is the energy input into the system per unit time, C is the energy cost of maintenance and replacement per unit time per individual, b is the energy cost per individual per unit time of interacting with a conspecific, N is the number of individuals, and r is the conversion rate of energy into individuals. Schoener extends this model to two species competition:

$$dN_i/dt = r_iN_i[(I/N_i) - C_i - b_iN_i - d_iN_j],\qquad i \neq j,\qquad(2)$$

where the other parameters are the same as before, and where d_i is the energy cost per individual of interacting with a member of species j.

We have no comments on the intuitive or mechanistic basis of Schoener's derivation. We shall only comment on how well Eq. (2) accounts phenomenologically for the results we obtained in our *Drosophila* system. First note that, insofar as form is concerned, both Eq. (1) and Eq. (2) have an "excess" parameter: r may be incorporated into the other parameters through a suitable normalization. In our original analysis we did, in fact, consider models of the form

$$dN_i/dt = N_i[(I_i/N_i^{F_i}) - C_i - b_iN_i - d_iN_j)].\qquad(3)$$

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This model differs from Schoener's in two regards. First, the exponent F_i may be different from 1. Second, the parameter I may be different for the two populations. Schoener assumes that this parameter is the same for both populations, although relaxes this assumption in a later work (Schoener, 1974). Constraining it to be the same for both species introduces insuperable difficulties in obtaining least-squares estimates. Unfortunately, we could not fit the data for $F = 1$, since our least-squares algorithm required that the fitted function go through the origin, i.e., that the growth of a population be zero when its density is zero (which we considered eminently reasonable). Schoener's model has its *maximum* growth when the population density is zero.

We fitted the *Drosophila* data for values of $F = 0.3$, 0.5 and 0.7. For both *D. willistoni* and *D. pseudoobscura* the best fit, in terms of R^2, the multiple correlation coefficient, came with $F = 0.3$ and the worst fit came with $F = 0.7$. Thus, as F approached 1, that is, as the model became more and more like Eq. (2), the fit got worse. And in any case, the R^2 statistic was consistently lower than what we got with other models (though it was much higher than the R^2 for the Lotka–Volterra model).

We have recently used a different algorithm to fit our 19 vector *Drosophila* data to Schoener's model. This algorithm does not weight the vectors by their variance, as we did in our earlier fitting, but this is of no great importance.

Some interesting things have turned up. The estimates of I_i for the two populations are less than 4% different in value—which agrees with the assumption of Schoener's original model. Second, the significances of the C parameters are very low—their t-values are around 0.5. C for one population is positive, but negative for the other, and both are close to zero. This implies that the simplified model

$$dN_i/dt = N_i[(I_i/N_i) - b_i N_i - d_i N_j],$$

would give almost as good a fit to the data. This is a three parameter model that fits the data better than the Lotka-Volterra model.

Schoener's model has the difficulty that the maximum growth occurs at a population density of zero, which means that the per individual growth rate is infinite at that density. Moreover, this maximum growth point, which corresponds to the inflection point on a curve of density vs. time, is fixed. Schoener understands this difficulty. In fact, he cites a large body of experimental data suggesting that the inflection point in most studies of population growth occurs at a value of N greater than $K/2$. Schoener solves this problem by having populations shift models midstream in their growth. This greatly complicates the mathematics. It calls for two models, each with its own set of parameters, plus an additional parameter to mediate the transition.

The model we found that best fits the data from the *Drosophila* competition

experiments adds a single parameter to the Lotka-Volterra competition equations:

$$\frac{dN_i}{dt} = r_i N_i \left[1 - \left(\frac{N_i}{K_i} \right)^{\theta_i} - \frac{\alpha_{ij} N_j}{K_i} \right], \qquad i \neq j, \tag{5}$$

where θ_i governs the asymmetry of the single species growth curves—the plot of dN_i/dt vs. N_i. Changes in the inflection point from $K/2$ are thus easily modeled by changes in θ; $\theta_i > 1$ for inflection points above $K/2$, $\theta_i < 1$ for inflection points less than $K/2$.

In summary, Schoener's model does not explain as much of the variance in the data from *Drosophila* competition as our θ model, and it has one parameter that is highly insignificant (though this parameter may be eliminated without appreciably altering the nature of Schoener's model). In addition, his model is less general than ours. Nonetheless, a very interesting prediction from his model—that I, the input of energy, should be the same for both populations—was borne out by our least-squares fitting analysis. We suggest, therefore, that our model may have more phenomonological accuracy and generality, but that there may be some interesting mechanistic truths in Schoener's.

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