



Global Models of Growth and Competition

(population dynamics/niche theory/coexistence)

MICHAEL E. GILPIN AND FRANCISCO J. AYALA

Department of Entomology and Department of Genetics, University of California, Davis, Calif. 95616

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ABSTRACT Very precise data on the dynamics of a competitive system of two species of *Drosophila* have been obtained. By a curvilinear regression approach, analytical models of competition have been fitted. By statistical and biological criteria of simplicity, reality, generality, and accuracy, the best of these models has been chosen. This model represents an extension of the Lotka–Volterra model of competition; it adds a fourth parameter that controls the degree of nonlinearity in intraspecific growth regulation. It represents a similar extension of the logistic model of population growth.

Population ecology is at a Keplerian stage of development. Much of the present theory is based on idealized linear interactions (which are valid first-order approximations of more general interaction), somewhat as pre-Keplerian astronomy was based on idealized circular motions (which approximate ellipses). For interspecies competition, the present need is to obtain precise data that disclose the global dynamics of real competition systems, that is, the rates of population growth at any combination of population densities. Simple but general analytical models may then be sought to represent such systems. Only if this attempt achieves success should the Newton-like effort of producing a law for the repulsive “forces” of intraspecies and interspecies competition be undertaken, though the obviously pluralistic nature of biological mechanisms could make this effort profitless.

In the 1920s, the linear model of competition was proposed independently by Lotka (1) and Volterra (2); it is

$$\frac{dN_i}{dt} = r_i N_i (1 - N_i/K_i - \alpha_{ij} N_j/K_i),$$

$$i, j = 1, 2, i \neq j. \quad [1]$$

N_i is the population density of the i th species; r_i is the exponential rate of growth of the i th species when both the i th and j th population densities are low; K_i is the carrying capacity of the i th species in the absence of its competitor, the j th species; and α_{ij} is the linear reduction (in terms of K_i) of the i th species' rate of growth by its competitor, the j th species. This model and other analytical models of competition ignore time lags, thresholds, and stochastic effects; but this is necessary if the mathematics are to be kept tractable and should lead to no difficulties if not forgotten.

Volterra, in the absence of any competition data whatsoever, felt that the above model could be globally valid. Lotka indicated that the correct competition model was likely to be nonlinear; but by making a Taylor's series expansion about the point of equilibrium and dropping the higher order terms, he was able to arrive at the same model of competition as an approximation valid in a “neighborhood” of the equilibrium point. Levins (3) and MacArthur (4) have added to the importance of this linear model by basing their niche theory on it, and they have provided independent formulas to calculate the K and α parameters. Vandermeer (5) has used the α s of the Lotka–Volterra competition equations to determine the “community matrix” of a competition ecosystem. But such epitheory does nothing to validate the linear model.

In 1934, Gause (9) determined the dynamics of yeast and protozoan competition and was thereby able to validate the linear competition model. But no similar effort has been made to evaluate the linear model for arthropod or vertebrate competition until this work.

In testing the linear model with biological data, an exact fit is not expected, for there is simply too much unavoidable heterogeneity. The important question is this: Does a *slightly* more complicated model yield *significantly* more accurate results? To return to the Keplerian analogy, the equation for an ellipse is only slightly more complicated than the equation for a circle (it adds one additional parameter), yet the significance of elliptical orbit was profoundly important for the development of subsequent gravitation theory.

Competitive *Drosophila* systems can be easily and precisely studied; they serve as an excellent point of departure to obtain information on the global dynamics of competitive systems. It has already been established that one such system does not fit the linear Lotka–Volterra model, for the locations of its single- and two-species points of equilibrium do not satisfy a necessary condition of coexistence derived for this model (6). The study of seven additional *Drosophila* systems has confirmed the inadequacy of the Lotka–Volterra model (10). The inclusion of nonlinear terms in an analytic competition model explains the anomalous location of stable points of equilibrium (7).

We have now made additional experiments that provide rather complete information on the global dynamics of a *Drosophila* system. The experiments are designed to estimate the “vectors” describing the change in numbers during a fixed time interval from advisedly chosen initial combinations of two species. The species used are *Drosophila willistoni* (strain M11) and *D. pseudoobscura* (strain 211). Adult flies in the desired densities are introduced into a 0.24-liter culture bottle containing a measured amount of food. After 7 days the surviving adults (“survivors”) are counted and discarded; the flies of the two species that emerge in that bottle during the following 4 weeks (“recruits”) are also counted. In a phase plane defined by the coordinates representing the numbers of the two species, a vector is drawn from the point representing the initial state to the point representing “survivors + recruits” for the two species. The resulting vector thus estimates the change in numbers (ΔN) for a change in time (Δt) of 1 week that would occur in a continuous population [main-

TABLE 1. Regression analysis of models A and B

	<i>Drosophila willistoni</i>	<i>Drosophila pseudoobscura</i>
<i>Experimental values</i>		
Carrying capacity	1421 ± 32	772 ± 20
Equilibrium density	657 ± 18	399 ± 11
<i>Model A</i>		
<i>r</i>	1.496 ± 0.167	4.513 ± 0.259
<i>K</i>	1332 ± 128	791 ± 43
α	0.713 ± 0.077	0.0869 ± 0.0062
θ	0.35 ± 0.04	0.12 ± 0.02
Carrying capacity	1332	791
Equilibrium density	616	441
Explained variance	92.9%	95.3%
Total error	166	
<i>Model B</i>		
<i>r</i>	1.006 ± 0.094	1.119 ± 0.094
<i>K</i>	953 ± 88	521 ± 48
α	0.806 ± 0.065	0.223 ± 0.017
β	-0.000210 ± 0.000029	-0.000376 ± 0.000048
Carrying capacity	1392	990
Equilibrium density	439	553
Explained variance	95.9%	94.9%
Total error	513	

The parameter values are regression estimates ± standard errors. The experimental values are means ± standard errors. *Total error* is the sum of the three distances between experimental and estimated carrying capacities and point of equilibrium; it is defined: Total error = $|K_w^e - K_w^m| + |K_p^e - K_p^m| + [(\bar{N}_w^e - \bar{N}_w^m)^2 + (\bar{N}_p^e - \bar{N}_p^m)^2]^{1/2}$, where superscript *e* signifies an experimental value and superscript *m* signifies an estimation from the model, and where the subscripts denote the species.

tained by serial transfer (6)] at the same state. All experiments are conducted at $21.5 \pm 0.5^\circ$. Nineteen such vectors were obtained and are shown in Fig. 1, where for clarity, the lengths of the vectors have been reduced by two-thirds. Each vector is the mean of about 17 replications; the standard errors for the means are small (10). For each species, a line may be drawn (a “zero isocline”) that separates the phase plane region of positive growth from the region of negative growth. Drawn by visual inspection, these two lines are shown on Fig. 1. The single-species equilibrium (carrying capacity) of a species occurs where its zero isocline intersects its species axis; the two-species equilibrium occurs where the two zero isoclines intersect. The slopes of the two zero isoclines at the point of equilibrium indicate that the equilibrium is stable (7). For the two single-species systems and the two-species system, three replicate continuous-time populations were maintained by serial transfer for about a year. A time average from week 12 to the final week established observed values for the two carrying capacities (K_p^e and K_w^e) and for the two-species equilibrium point ($\bar{N}_p^e$, $\bar{N}_w^e$). These values are displayed as solid circles on Fig. 1. The close agreement between these observed points

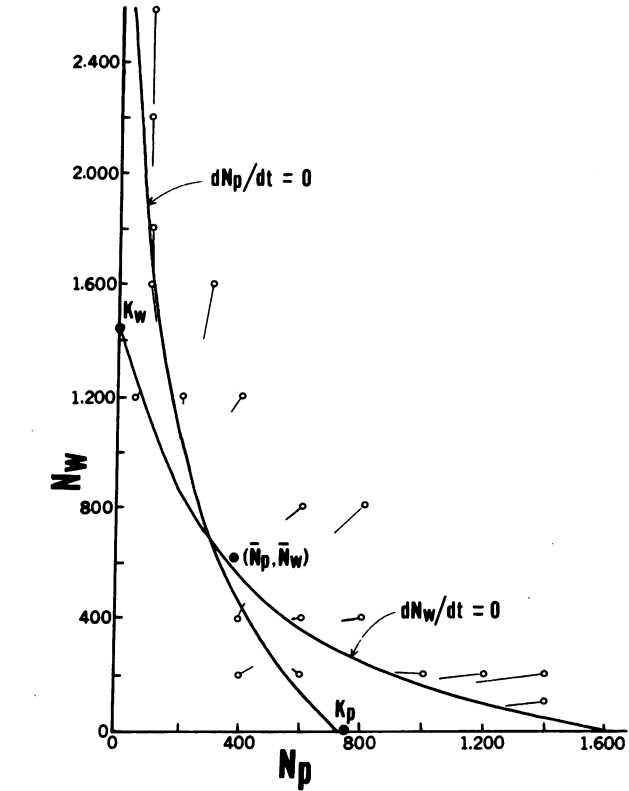


FIG. 1. The phase plane description of the dynamics of a *Drosophila willistoni* and *D. pseudoobscura* competitive system as experimentally determined. The open circles represent initial densities of the two species. The directed line segments (or vectors) from the open circles show the changes in the system after 1 week's time. For clarity, these vectors have been reduced to one-third of their true length. The solid lines are the zero isoclines for the two species. They separate the phase plane region of positive growth from the phase plane region of negative growth; these lines have been drawn from visual inspection of the data. The solid circles represent the carrying capacities and equilibrium point of the system as determined by independent, continuous-time experiments.

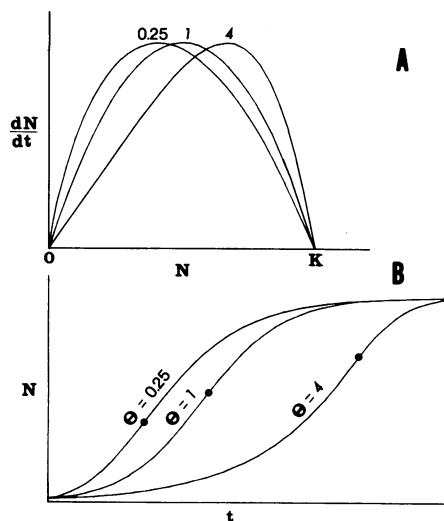


FIG. 2. (A) Model A growth rates as a function of N for three different populations. All populations have the same carrying capacity, K , and the same maximum population growth rate. θ values are as indicated. Their r values, which are the slopes of the growth line at the origin, are inversely correlated with θ . (B) Population size as a function of time for the above three populations; these are obtained by integrating the growth rate, dN/dt , over time. At the inflection points, indicated by the solid circles, all growth curves have the same (maximum) slope. The invertebrate curve ($\theta = 0.25$) reaches its maximum growth rate early and gradually decelerates towards the carrying capacity. The vertebrate curve ($\theta = 4$) grows exponentially until it is almost at its carrying capacity, and then decelerates rapidly.

and the points obtained from the vector information indicates the equivalence of time averages and averages over ensembles, and thus establishes a kind of ergodic theorem for population biology.

An analytical model of competition is a set of differential equations of the following form:

$$\frac{dN_i}{dt} = D_i(N_i, N_j; r_i, K_i, \alpha_{ij}, \beta_{ij}, \dots). \quad [2]$$

The N s are state variables that give the numbers or densities of the two populations; the other symbols in Eq. 2 are parameters by which the state variables interact to give the time rate of change of the state variables.

The vectors of Fig. 1 estimate values of the functions D_i at 19 different points (N_i, N_j). Once the form of the D_i function of Eq. 2 is explicitly stated, the values of the parameters may be found by minimizing the sum of the square of the errors between the experimental data and the model estimates of dN_i/dt . This procedure also produces the following statistics: the level of significance of individual parameters, and the amount of experimental variance the whole model explains.

We tested about 20 different competition models by fitting each to the data of Fig. 1(10). To decide on the adequacy of a model we used the following four criteria:

(1) Simplicity. The model should contain the minimum number of parameters that are necessary to

account for the observed results. Thus, any parameters that are not statistically significant at the 95% level are not acceptable; also, if a model with fewer parameters explains as much (or more) of the experimental variance as a model with more parameters, the former is considered preferable.

(2) Reality. All of the parameters of the model should have biological interpretation.

(3) Generality. The model should be as general as possible. In particular, it should have the Lotka-Volterra model as a special case, since this model adequately models competition between microorganisms.

(4) Accuracy. (a) The explained variance should be as close to 100% as possible. (b) The shape of the predicted zero isoclines of the model should be similar to those drawn by visual inspection in Fig. 1. (c) The location of the predicted carrying capacities and the predicted point of the two-species equilibrium should agree with those of the year-long continuous-time experiments (i.e., the solid circles of Fig. 1).

We found two models each with four parameters—one more than the Lotka-Volterra model—that satisfied the above criteria. These models are:

$$(A) \quad \frac{dN_i}{dt} = r_i N_i (1 - (N_i/K_i)^{\theta_i} - \alpha_{ij} N_j/K_i). \quad [3]$$

$$(B) \quad \frac{dN_i}{dt} = r_i N_i (1 - N_i/K_i - \alpha_{ij} N_j/K_i - \beta_i N_i^2/K_i). \quad [4]$$

The parameters of these models do not necessarily have any biological significance; an attempt to justify them will be made below. Nonetheless, both models are relatively simple with only four parameters, that is, one more than the Lotka-Volterra model. Both models are general and have the Lotka-Volterra model as a special case: for model A when $\theta_i = 1$, and for model B when $\beta_i = 0$. Both models explain about 95% of the experimental variance [models with five or more parameters explain very little more (10)] and all the parameters of both models are significant at the 99% level (Table 1). Both models yield zero isoclines and equilibrium points that resemble those of Fig. 1. On the grounds of simplicity, generality and accuracy, it is therefore impossible to choose between the two models.

We believe, however, that the correlation between model B and the data is spurious. On the basis of biological reality, model B may be rejected. Because the parameter β is negative for both *D. pseudoobscura* and *D. willistoni*, the biological reality of this parameter must be social cooperation or facilitation that increases with the square of population density. This is unlikely. There is no strongly increasing social cooperation between a thousand or so *Drosophila* crowded in a 0.24-liter culture bottle. Furthermore, model B has serious mathematical weaknesses. For instance, it predicts

positive growth for both species at very high densities, and its zero isoclines, which are parabolas, cannot be bent close enough to the origin to explain the locations of some of the equilibrium points that have been observed. Consequently, only model A can be the kind of model we are seeking.

Model A has no mathematical weaknesses. The interpretation of the parameters is straight forward. r_i is the exponential rate of growth of the i th species when the population densities of the i th and j th species are low; K_i is the carrying capacity of the i th species in the absence of its competitor, the j th species; α_{ij} is the linear reduction (in terms of K_i) of the growth rate of the i th species by its competitor, the j th species; and θ_i gives the asymmetry of the single-species growth of the i th species.

In the absence of competition, that is when $\alpha = 0$, model A models single-species growth, and it represents a generalization of the logistic growth equation. For logistic growth, the function that relates growth rate to density is a parabola that intersects the density axis at 0 and K and is symmetrical about $K/2$. The addition of the parameter θ in model A removes this restriction of symmetry: the maximum rate of growth may be at values that are either greater than $K/2$ or less than $K/2$ (Fig. 2).

When N in Eq. 3 denotes adult individuals, and eggs, larvae, pupae, etc. are ignored, we believe that invertebrate populations will, in general, have a θ value of less than 1; and we suggest that vertebrate populations will have a θ value greater than one. The growth of populations of vertebrates is often limited by social methods (8) such as territory and dominance. Such methods, when brought into play, tend to stop population growth rather abruptly, and not in the continuously linear fashion that obtains for the Lotka-Volterra model, that is when $\theta = 1$.

For model A, a sufficient condition for competitive coexistence (and a condition that would almost certainly

be biologically necessary, though not mathematically necessary) is

$$K_1 < K_2/\alpha_{21} \text{ and } K_2 < K_1/\alpha_{12}. \quad [5]$$

This sufficient condition for coexistence is identical to the necessary and sufficient conditions of the Lotka-Volterra model.

Finally, model A is a linear model of interspecies competition. It is the intraspecific competition (or growth regulation) that is nonlinear. The regression estimates of the linear α s of model A are surprisingly low ($\alpha_{pv} = 0.09$ and $\alpha_{wp} = 0.71$). If these are taken to be measures of "niche overlap," it would indicate the *D. willistoni* niche has only a 9% overlap on the *D. pseudoobscura* niche despite the severe crowding. This linearity of interspecies competition indicates that the concept of a community matrix may be valid for interspecific interactions, that is, the off-diagonal terms in this matrix.

Model A is a relatively simple extension of the Lotka-Volterra competition model that substantially improves the modeling of *Drosophila* competition. If this model proves equally useful with other organisms, model A may be advanced as a globally accurate model of intraspecific and interspecific competition.

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1. Lotka, A. (1924) *Elements of Physical Biology* (Williams and Wilkins, Baltimore, Md.).
2. Volterra, V. (1931) *Lecons Sur la Theorie Mathematique de la Lutte pour la Vie* (Gauthier-Villars, Paris).
3. Levins, R. (1968) *Evolution in Changing Environments* (Princeton University Press, Princeton, N.J.).
4. MacArthur, R. H. (1972) *Geographical Ecology* (Harper and Row, New York).
5. Vandermeer, J. H. (1970) *Amer. Natur.* **104**, 73-83.
6. Ayala, F. J. (1969) *Nature* **224**, 1076-1079.
7. Gilpin, M. E. & Justice, K. E. (1972) *Nature* **236**, 273-303.
8. Wynne-Edwards, V. C. (1962) *Animal Dispersion in Relation to Social Behavior* (Oliver and Boyd, London).
9. Gause, G. F. (1934) *The Struggle for Existence* (Reprinted 1971, Dover, New York).
10. Ayala, F. J., Gilpin, M. E. & Ehrenfeld, J. G. (1973) *Theoretical Population Biology* **4**, 331-356.