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Journal

Proceedings of the National Academy of Sciences of the United States of America, 78(3)

ISSN

0027-8424

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Publication Date

1981-03-01

DOI

10.1073/pnas.78.3.1972

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Peer reviewed

Boundary-layer model for the population dynamics of single species

(population growth/logistic equation/ θ model /*Drosophila*)

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Contributed by Francisco J. Ayala, November 25, 1980

ABSTRACT We develop a new discrete-time model, called the boundary-layer model, to describe the dynamics of single species that have a capacity for fast growth at very low population densities. The model explicitly separates the dynamics of the population at very low densities (within the "boundary layer") and at high densities. The boundary-layer model provides a better fit than other models such as the logistic or the θ model to data from experimental populations of *Drosophila willistoni* and *D. pseudoobscura*.

A fundamental problem in theoretical ecology is the description of the dynamics of single-species populations. Approaches to this problem can be traced to Verhulst, Pearl, Lotka, and Volterra (for recent reviews, see refs. 1 and 2). The logistic equation and simple modifications of it are the models most commonly used to describe the population dynamics of single species, but they fail to describe adequately the dynamics of even simple laboratory populations of *Drosophila*. The θ model (3), which adds a third parameter (θ) to the two (r and K) used in the logistic equation, has been shown to provide a reasonably good fit to experimental data, but it fails to account for the very fast rate of population growth observed in some organisms when their density is very low.

The general form of the logistic and related models is an equation for exponential growth multiplied by a term that expresses intraspecific competition. In the present paper, we develop a new model that explicitly separates population growth into two regions. One region encompasses the population densities at which fecundity is the main limiting factor of population growth—i.e., population densities below what we shall call the "fecundity-saturation" of the environment. The second region encompasses the population densities at which survival in competition for limited resources is the limiting factor—i.e., densities above the capacity of the population for fecundity-saturation of the environment. This new model contains three parameters to which a direct biological interpretation can be given and provides a strikingly better fit than does the logistic or the θ model to certain data from laboratory populations of *Drosophila*.

THE MODEL

The model herein developed is a discrete-time model, of the form

$$N_{t+1} = g(N_t), \quad [1]$$

where N_t is the size of the population at time t . A discrete-time model is used in order to simplify the derivation as well as to

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make possible its application to laboratory experiments that provide discrete-time data.

First, we consider the basic features that the model should have. The processes determining the number of organisms at the next census time, in terms of the current population size, are separated into several categories depending on the current population size. At very low population densities (on the order of 1% of the carrying capacity), the population does not have the capacity for fecundity-saturation of the environment and the limitation to growth is determined by fecundity. The range of densities below fecundity-saturation will be called the "boundary layer." Within the boundary layer, population size from one census to the next increases rapidly as a function of current population size. At all but these very low densities, the fecundity of the organisms is high enough to saturate the available resources; the environment is then fecundity-saturated, and survival in competition for limited resources is the major determinant of population size from one census to the next. The form of the model at densities above the fecundity-saturation of the environment is the outer solution, which provides for slow changes in population density from census to census. Between the boundary layer and the region governed by the outer solution, there is a transition region where both fecundity and survival play roles.

Previous discrete models of population growth usually are discrete versions of the logistic equation (or of simple modifications of the logistic equation). The logistic equation is based upon a Taylor series, which is a reasonable way to approximate the right-hand side of Eq. 1 if the rate of population growth does not experience sudden changes as a function of population density. When sudden changes occur, it is appropriate to use a singular-perturbation approach (cf. refs. 4 and 5). The form of our model is therefore based upon ideas from singular-perturbation theory.

It is simpler to present our model in terms of a nondimensional population size, defined as

$$n = N/K. \quad [2]$$

This transformation simply ensures that at the carrying capacity ($N = K$), n is 1.

We will advance, first, the form of the model within the boundary layer, then present the outer solution, and, finally, describe how to integrate these two components of the model. This integration will allow us to obtain the solution in the transition region and to achieve a single model valid for all population densities.

In the boundary layer, when population density is very low, the model has the form

$$n_{t+1} = c(1 - e^{-n/\epsilon}), \quad [3]$$

where ϵ is a small parameter which measures the magnitude of the boundary layer [i.e., the fraction of the range of population densities from 0 to K within which the environment is not fecundity-saturated (see below)] and the constant c , which will be specified later, reflects the population size at the census immediately after the fecundity-saturation is reached.

The general form of Eq. 3 incorporates the notion of diminishing returns for each additional individual added to the population. A model of such a form has been shown (3) to provide a good fit to data from experimental *Drosophila* populations.

For all values of n_t except very low ones (i.e., except those within the boundary layer), we will model population growth by

$$n_{t+1} = e^{b(1-n_t)} \quad [4]$$

Eq. 4 is a general exponential model that satisfies the condition that if n_t is 1, so is n_{t+1} . The constant b reflects density dependence in the region of the outer solution.

Note that Eq. 3 does not satisfy the condition that n_{t+1} is 1 whenever n_t is equal to 1 and that Eq. 4 does not satisfy the condition that n_{t+1} is 0 whenever n_t is 0. Therefore, neither equation alone provides a uniformly valid model. In order to obtain such a valid model, we must "match" Eq. 3 with Eq. 4 (5).

We will specify that the limit of the right-hand side of Eq. 3 as $n_t/\epsilon \rightarrow \infty$ be also the limit of the right-hand side of Eq. 4 as $n_t \rightarrow 0$. We then add the two solutions and subtract their common part (i.e., the limit above) in order to obtain a single solution or model. This procedure forces c in Eq. 3 to be e^b and yields the composite model

$$n_{t+1} = e^b(1 - e^{-n_t/\epsilon}) + e^{b(1-n_t)} - e^b \quad [5]$$

This can be rewritten as

$$n_{t+1} = e^b(e^{-bn_t} - e^{-n_t/\epsilon}), \quad [6]$$

or

$$N_{t+1} = Ke^b(e^{-bN_t/K} - e^{-N_t/K\epsilon}). \quad [7]$$

Eq. 7 is the model that we sought.

The value of r , which measures the discrete-time intrinsic rate of growth in the logistic equation, can be approximated closely by taking the limit of n_{t+1}/n_t in Eq. 3 as $n_t \rightarrow 0$, namely

$$e^r \approx e^b/\epsilon \quad [8]$$

or

$$r \approx b - \ln \epsilon. \quad [9]$$

Note that very small values of ϵ correspond to very large values of r , an inverse relation that we would expect because the greater the intrinsic capacity of growth (r), the lower the density at which the environment will be fecundity-saturated (i.e., the smaller the range of densities encompassed within the boundary layer).

By taking the derivative of the right-hand side of Eq. 7, we observe that the equilibrium point, given by

$$\hat{N} \approx K, \quad [10]$$

is stable if

$$-1 < b < 1, \quad [11]$$

that is, whenever the population size at the generation after saturation lies between K/e and Ke , a condition that will almost certainly be satisfied in any real populations. However, if b is negative, the model has a second, unstable, equilibrium at very

high population levels. This simply implies that the applicability of the model is restricted to population sizes less than several times the carrying capacity.

If b is positive, the population overshoots K , whereas if b is negative, K is approached monotonically. This is because b is approximately the natural logarithm of the nondimensional measure of population size at the census after the population reaches the fecundity-saturation density (and the natural logarithm of the nondimensional carrying capacity is, of course, 0).

It should be noted that the form of the model advanced here was suggested by the approximate solution to the singularly perturbed boundary-value problem (4, 5):

$$\begin{aligned} \epsilon \frac{d^2 y}{dx^2} + \frac{dy}{dx} + by &= 0; \quad 0 < x < 1, \quad 0 < \epsilon \ll 1 \\ y(0) &= 0 \\ y(1) &= 1. \end{aligned} \quad [12]$$

We identify y with n_{t+1} , and x with n_t . This solution has the desired properties and requires only three parameters, the same as the θ model and only one more than the logistic model.

EXPERIMENTAL RESULTS AND DISCUSSION

We now describe an application of the model by using experimental laboratory populations of *Drosophila*. The experiments were carried out with each of two species, *D. willistoni* and *D. pseudoobscura*, using the type-2 experimental procedure (3). Briefly, a specified number of adults, N_t , were allowed to lay eggs for 1 week in a half-pint culture with fresh medium. After 1 week, the survivors were counted and discarded; the adults emerging from the culture were then recorded at 1 week intervals over the following 4–5 weeks, so as to obtain the complete first-generation progeny while avoiding a second generation. The sum of the survivors plus the emerging adults estimates the number of individuals after 1 week, N_{t+1} , in a population maintained by serial transfer [type-1 experiments (3)]. The change in numbers after 1 week ($\Delta N = N_{t+1} - N_t$) for various initial numbers is given in the second column of Tables 1 and 2 and in Fig. 1.

The experimental details are given in ref. 6, where fits to the data are made by using discrete-time versions of the logistic

Table 1. Dynamics of experimental populations of *D. willistoni* and best fit by the boundary-layer model using the parameters given in Table 3.

Initial number	ΔN	Best fit of model to ΔN
8	415 ± 49	428
16	763 ± 79	678
32	905 ± 29	903
64	937 ± 51	982
96	948 ± 75	959
128	872 ± 49	925
192	781 ± 36	852
256	689 ± 37	779
384	614 ± 39	634
512	595 ± 49	489
768	439 ± 58	200
1024	87 ± 56	-88
1280	-90 ± 64	-374
1536	-526 ± 49	-660
1792	-1068 ± 50	-945
2048	-1360 ± 39	-1229

The change in population numbers after 1 week (ΔN) is given as the mean ± SEM of 20 observations.

Table 2. Dynamics of experimental populations of *D. pseudoobscura* and best fit by the boundary-layer model using the parameters given in Table 3.

Initial number	ΔN	Best fit of model to ΔN
8	264 ± 21	280
16	327 ± 14	298
32	282 ± 33	287
64	213 ± 19	262
96	185 ± 20	236
128	194 ± 19	211
192	95 ± 23	160
256	98 ± 19	110
384	64 ± 18	12
512	-22 ± 25	-84
768	-239 ± 17	-267
1024	-462 ± 34	-438
1280	-655 ± 42	-594

The change in population numbers after 1 week (ΔN) is given as the mean ± SEM of 20 observations.

model, the θ model, and other modifications of the logistic equation. In the case of nonlinear models, numerical techniques were used to optimize the following goodness-of-fit measure (3):

$$R^2 = 1 - \frac{\left[\sum_{i=1}^m (\Delta N(i) - \Delta \bar{N}(i))^2 / \sigma_i^2 \right]}{\left[\sum_{i=1}^m (\Delta N(i))^2 / \sigma_i^2 \right]}, \quad [13]$$

where $\Delta N(i)$ and σ_i^2 are the mean and variance of the experimental observations and $\Delta \bar{N}(i)$ is the prediction from the model. The m different values of N_i are listed in Tables 1 and 2.

The largest values of R^2 obtained in ref. 6 for the logistic, the θ , and related models are around 0.70. In contrast, a similar numerical optimization of R^2 for the boundary-layer model yields values of R^2 above 0.97. This considerable improvement occurs in spite of the fact that the boundary layer model has no more parameters than the θ model or some other models used in ref. 6. The values of ΔN predicted by the boundary-layer model are given in the third column of Tables 1 and 2 and in Fig. 1. The values of the various parameters for each one of the two species are given in Table 3.

It should be noted that experimental data of the kind reported here can be used to obtain estimates of "growth rate" (7) for a population at various densities. The θ model has been shown to provide good fit for the growth rate of experimental populations of *Drosophila*, but we are interested in a model that provides good fit to "net productivity" data (see ref. 7)—i.e., to the data directly obtained in type-2 experiments—because the question whether or not growth rate measures population dynamics better than net productivity is moot.

The behavior of the present model as a function of ϵ , which measures the width of the boundary layer, is of great interest. For either species, the value of ϵ is truly small—namely, smaller than 0.02—indicating that fecundity-saturation occurs at densities lesser than 2% of the carrying capacity (K). It should be noted, however, that the dependence of R^2 on ϵ is quite weak, because of the scarcity of data points in the boundary layer.

The value of b is positive for *D. willistoni*, indicating that the population would overshoot in its approach to K ; it is negative for *D. pseudoobscura*, indicating monotonic increase for this species. In both cases, b is close to 0, evidencing stability in

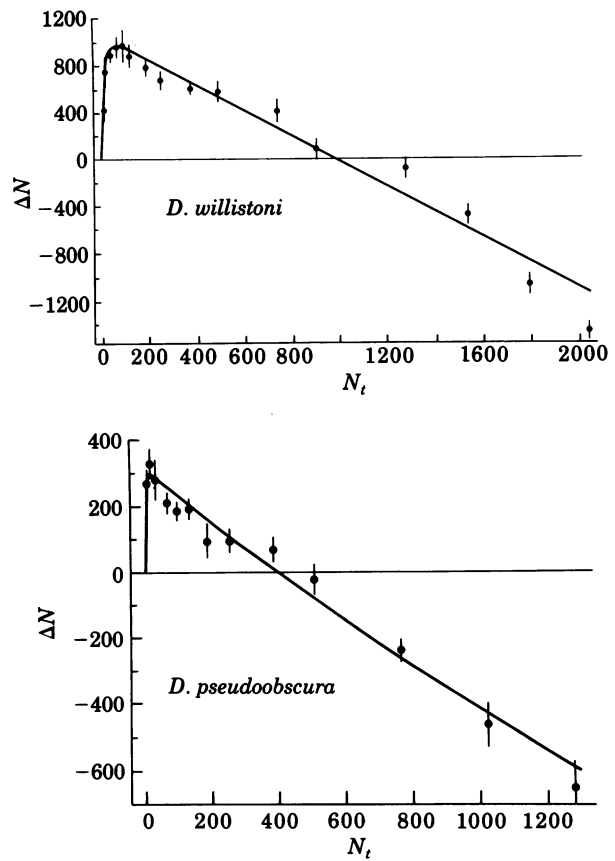


FIG. 1. Change in numbers (ΔN) as a function of density (N_t) in experimental populations of *D. willistoni* (Upper) and *D. pseudoobscura* (Lower). The error bars indicate 2 SEM (based on 20 observations) on each side of the points. The solid line represents the best fit of the boundary-layer model.

spite of the fact that r , calculated from Eq. 9, is greater than 4 in both cases (see Table 3).

Although the values of r for the two species (4.24 for *D. willistoni* and 4.56 for *D. pseudoobscura*) are similar, the value of ϵ for *D. pseudoobscura* is half that for *D. willistoni*. The value of ϵ may be a better indicator of colonizing ability than the value of r because ϵ indicates how quickly, relative to K , a population reaches its fecundity-saturation density. *D. pseudoobscura* is a temperate species that maintains very low densities during much of the year but multiplies rapidly in the spring, whereas *D. willistoni* is a tropical species with relatively small fluctuations in population size throughout the year. The low value of ϵ obtained for *D. pseudoobscura* is consistent with the notion that this species may be r -selected, so that it can rapidly reach its fecundity-saturation density whenever the environmental conditions are favorable.

Some properties of the present model in relation to other models deserve attention. The logistic and related models use the parameters r and K ; the θ -model uses, in addition, a "shape" parameter, θ . Of these parameters, only K is directly used in the boundary-layer model. The exponential capacity for growth,

Table 3. Parameter values obtained in the best fit of the boundary-layer model to the data in Tables 1 and 2

	R^2	ϵ	K	b	r
<i>D. willistoni</i>	0.982	0.0161	946.06	0.114	4.24
<i>D. pseudoobscura</i>	0.974	0.0081	400.00	-0.255	4.56

r , has been replaced by a combination of two parameters: ε , which measures the fractional value of K at which the environment is fecundity-saturated (and, hence, where the maximum rate of growth is approached), and b , a measure of population density after fecundity-saturation. The form of the model includes the property that the maximum rate of growth of a population need not be at half the carrying capacity (as is the case for the logistic model) but may occur at a small fraction of the carrying capacity—a situation that appears to be almost universal among arthropods (8). The θ model also makes it possible to have the maximum rate of growth at a value other than $K/2$, but it cannot be at a density less than K/e ; this restriction does not occur in the present model.

An additional feature of the model is that it can yield a stable equilibrium even when the rate of population increase at very low densities is very high. This stands in marked contrast to the situation obtained for other simple difference-equation models (9, 10).

It seems likely that the boundary-layer model may provide a good description of the population dynamics of organisms with very high fecundity or growth-rate potential, for which the fecundity-saturation of the environment may occur at very low densities. Whether or not this conjecture will be corroborated must wait for future tests. The significance of the model will

also depend on the possibility of its extension to other problems, such as multispecies interactions and evolutionary questions.

Note Added in Proof. David J. Wollkind has kindly pointed out to us that our nondimensional Eq. 6 has previously been presented as a model of population growth—namely, equation 20c in ref. 11. In that paper, the authors proposed asymptotic models for various biological processes.

This work was supported by grants from the National Science Foundation (to A.H.) and the National Institutes of Health (to F.J.A.) and by a fellowship from the Fundación Juan March of Spain (to J.M.S.).

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