

BALANCED GROWTH RATES VS. BALANCED ACCELERATIONS AS CAUSES OF ECOLOGICAL EQUILIBRIA

L.R. Ginzburg, H.R. Akçakaya, D. Slice and L.B. Slobodkin
Department of Ecology and Evolution
State University of New York at Stony Brook,
Stony Brook, N.Y. 11794, U.S.A.

ABSTRACT. Trophic equilibrium has been traditionally viewed as a balance of causes influencing the growth rate of populations. It has been recently proposed to view it as a balance of causes influencing the acceleration of the population size (Ginzburg, 1986). Arguments in favor of the proposed view are presented. Data from population growth experiments with brown and green hydra as well as some literature data support the arguments.

1. INTRODUCTION

The abundance of organisms in a population depends on the total supply of resources (broadly defined). Population size therefore cannot be considered as a basic property of the organisms themselves. Growth rate is more significant as a characteristic of an organism, but it is also dependent on environmental circumstances. While maximal rate of exponential growth may characterise a species (Smith, 1954; Slobodkin, 1961), exponential population growth at any constant rate does not. It just implies that the environmental circumstances are staying constant. Population steady state is, of course, a special case of exponential growth at which the growth rate is zero. Thus, population size and its first logarithmic derivative, are highly dependent on environmental properties and cannot be expected to reveal very much about the properties of the organisms.

Growth rate may change due to either quantitative or qualitative changes in resources or in the physical environment. Might the pattern of change in growth rates (i.e, the second logarithmic derivative of population size) be a more basic property of a species? Perhaps our interpretation of ecological processes must be different depending on whether we focus on the first or the second derivative. The latter view has a rough analogy to 17th century physics in which focusing on the acceleration of motion rather than the speed permitted the abandonment of Aristotelian physics. We will attempt to defend this view by considering a simple case of starved population dynamics.

Consider a population placed in an environment without food. The growth (death) curves in such an environment will look as shown in

Figure 2. Let us consider this family of curves and concentrate attention on their curvature, or the rate with which growth rate declines. The variable of interest is the acceleration :

$$\frac{d^2}{dt^2} (\ln N)$$

Unlike the growth rate, $(1/N) dN/dt$, acceleration may not depend on a variety of environmental factors, which otherwise affect the growth rate. The acceleration of the population growth in the absence of food may in fact be a property of the species and not a function of the environment in which a population is placed. This is the assumption of the model proposed by Ginzburg (1986) in which the essence of the dynamics is reflected in the acceleration of population growth. Here, we propose a mechanism by which such a second-order model naturally arises by considering an intermediate energy-related variable.

Being slightly more general, consider a population in an environment unlimited in every respect, except for a fixed amount of food, S , available per unit time. Let us assume that per capita population growth rate, $(1/N) dN/dt$, is a function, G , of the amount of assimilated energy available to an average individual, x ; and the rate with which x changes is a function, F , of the amount of food, S , and the population size, N .

Function G describes the allocation of assimilated energy for reproduction, as opposed to "maintenance" (growth and basal metabolism), whereas function F describes the rate of assimilation of food, i.e., conversion of the available food into energy. Thus, function F incorporates foraging behavior and predation efficiency. We can represent the dynamics of this population with a set of two equations :

$$\frac{d}{dt} \ln N = \frac{1}{N} \frac{dN}{dt} = G(x) \quad (1)$$

$$\frac{dx}{dt} = F(S, N) \quad (2)$$

Here, $G(x)$ is a monotonically increasing function with the following properties. First, $G(0) = -\infty$, i.e., when there is no energy available, the population dies instantaneously. Second, as $x \rightarrow \infty$ the function reaches a maximum (Fig. 1). At this plateau, an increase in the available energy does not increase the per capita growth rate of the population. Examples of per capita population growth rate and fecundity of several species as a function of energy consumed per individual are given by Beddington, Hassell and Lawton (1976, Fig. 10 and 13) and by Beddington, Free and Lawton (1976, Fig. 2). These authors refer to 8 studies, 6 of which give a linear relation within the range observed, and 2 have the same shape as Fig. 1.

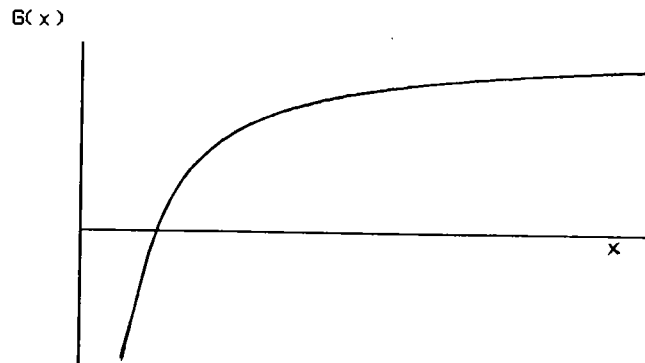


FIGURE 1: Per capita population growth rate as function of x .

Assuming x to be unobservable, we can deduce an equation which involves only the population size:

$$I \left(\frac{d}{dt} (\ln N) \right) \frac{d^2}{dt^2} (\ln N) = F(S, N) \quad (3)$$

where,

$$I \left(\frac{d}{dt} (\ln N) \right) = \left(\frac{dG}{dx} (G^{-1}(\frac{d}{dt} \ln N)) \right)^{-1} \quad (4)$$

abu
asc

is interpreted as the "inertia" of the population, determining the effect of a "force" resulting from a trophic interaction. Note that I is defined as a property which depends on the energy allocation policy of a given species but not on the interactions reflected in the function F .

Consider now a special case of population growth in the absence of food, $S=0$. Since energy is always expended at a certain rate for metabolism even if no food is eaten, we expect $dx/dt < 0$. Thus, $F(0, N) = -d < 0$. If, in addition, growth (death) rates are not too different from zero, we expect

$$\frac{d^2}{dt^2} \ln N = -a \quad (5)$$

where a is a constant which depends on d and $I(0)$.

The proposed equation implies that we expect accelerated decline in $\ln N$ in the absence of food in contrast to the traditional models which imply exponential decline. Moreover, if a number of populations of the same organism are placed in different environments without food, each population will respond by decreasing its growth rate, r , with an

approximately constant rate, $-a$.

2. MATERIALS AND METHODS

Populations of brown and green hydra were used in the experiments. Each population had an initial size of 5 individuals, which were put in petri dishes containing water samples taken from different tributaries of the Hudson River. Experiments were conducted using hydra taken from stock laboratory cultures. These were maintained in synthetic pond water and fed Artemia nauplii three times a week prior to the experiments. All the experiments were started on the day after feeding and the hydra were not fed during the course of an experiment. Two experiments (about 12 weeks apart) were run with each of brown and green hydra, using water samples from 51 locations, each with two replicates. The population sizes, along with other variables, were recorded once a week.

The observations (population sizes) for the two replicates for each location were geometrically averaged and 5 populations which did not have sufficient (i.e., at least two non-zero) data points were discarded. This resulted in a total of 101 populations for the two experiments with brown hydra, and 98 population for those with the green hydra.

Each population trajectory was analyzed by the least-squares fitting of the following non-linear model:

$$N = e^{(\ln N_0 + r_0 t + a t^2 / 2)} \quad (6)$$

where N is the population size (geometric mean of two replicates),

N_0 is the initial population size,

t is time (in weeks),

r_0 is the initial growth rate of the population, and

a is the rate of change of the growth rate (acceleration).

In order to have independent estimates of r_0 and a for each population, the model was fitted in two steps. In the first step, r_0 was fitted to each trajectory, using only the first three data points ($t = 0, 1, 2$), and assuming $a = 0$. This gave the estimates of the initial growth rate. In the second step, r_0 -estimates from the first step were substituted into the equation and the second parameter, a was fitted to each population trajectory separately. The second step was carried out with data point $t = 2, 3, \dots$ for green hydra and $t = 1, 2, \dots$ for brown hydra. Thus only one or two points were used for estimation of both r_0 and a , making the estimates as independent as possible. The result was 101 pairs of parameter (r_0 and a) estimates for populations of brown hydra and 98 pairs of estimates for populations of green hydra.

Two types of statistical tests were used to check the consistency

of the results with the proposed model. First, assuming that a is independent of the environment, the longevity of each population will be determined by r_0 and N_0 . Since N_0 is controlled, there should be a positive correlation between r_0 and longevity. To show this effect, populations were clustered with respect to their longevity and mean r_0 was calculated for each cluster.

The second way of testing the constancy of a is to compare the goodness of fit of a model with a constant a with that of a model with variable a (i.e., a specific a for each population). If a is truly constant, equally good fits should be obtained either by fitting both r_0 's and a 's to each trajectory, or by fitting only r_0 's with a constant a . In this more delicate test, three different residual mean square (MS_{res}) values were calculated for each trajectory and their distributions (within each type of hydra) were compared. The MS_{res} values were calculated by :

- (i) fitting both a 's and r_0 's to each trajectory.
- (ii) using a constant a (equal to the mean of a -estimates from (i)) for all populations and a specific r_0 for each population,
- (iii) using a constant r_0 (equal to the mean of the r_0 -estimates) for all populations and a specific a for each population.

Since the distributions are highly skewed, medians are used instead of means for comparisons. The null hypotheses for this test are that MS_{res} of (i) is not different than MS_{res} of (ii) and MS_{res} of (iii). If we can not reject the first null hypothesis but we can reject the second, this will be an even stronger suggestion that a is a species-specific constant while r_0 depends on the environment.

3. RESULTS OF THE ANALYSIS

Among populations of both organisms, there were those with negative initial r_0 's and those with positive initial r_0 's, although most populations of brown hydra were of the first type and most populations of green hydra of the second one. Table I summarizes the distributions of r_0 - and a -estimates for brown and green hydra. Distribution of r_0 has a significantly higher relative variation than that of a for both types of hydra. This result shows that in the absence of food in the environment, the relative rate of decline of a population is not constant as predicted by the logistic equation, but it changes with time, i.e., it decelerates. Moreover, r_0 varies between different environments whereas a is relatively constant for a given species. Both results are consistent with the proposed model.

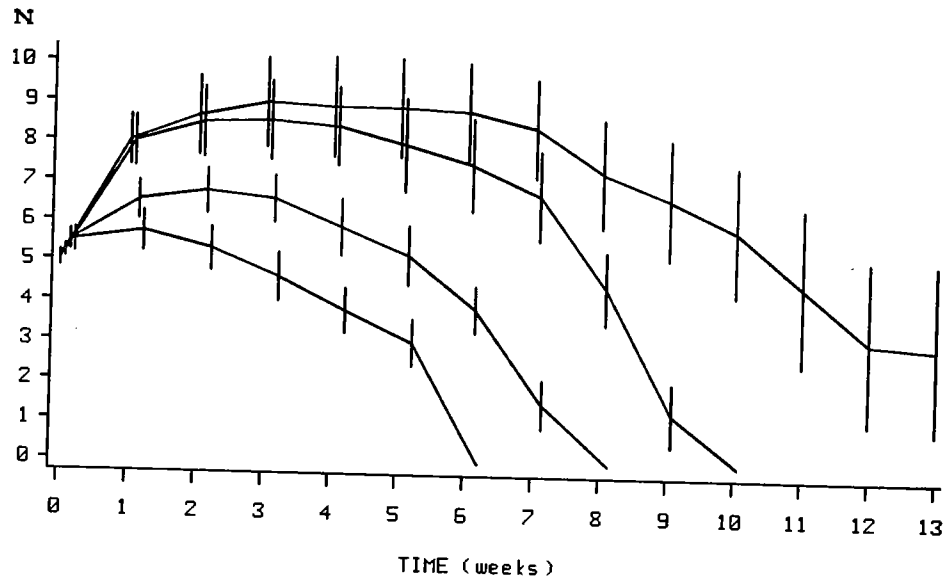


FIGURE 2: Mean and 95% confidence interval for the size of green hydra populations in each of the 4 clusters.

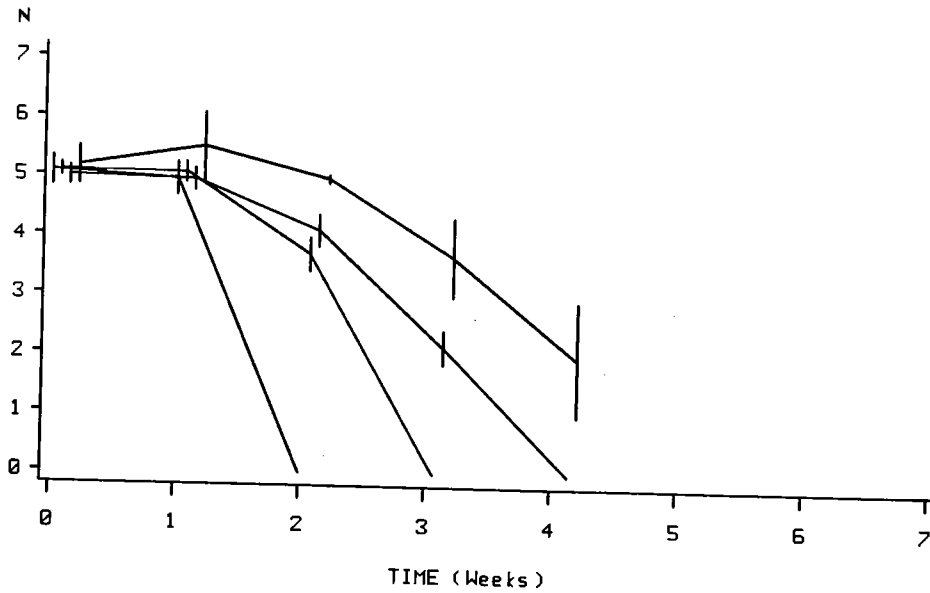


FIGURE 3: Mean and 95% confidence interval for the size of brown hydra populations in each of the 4 clusters.

TABLE I: r_o - and A - ESTIMATES FOR BROWN AND GREEN HYDRA

	Brown Hydra (n=101)		Green Hydra (n=98)	
	r_o	a	r_o	a
Mean	- 0.1751	- 0.1840	0.1406	- 0.0662
st. dev.	0.1882	0.0406	0.1713	0.0284
c.v.	107.5 %	22.1 %	121.8 %	43.0 %
s_v	± 13.76	± 1.63	± 17.33	± 3.59

c.v. = coefficient of variation

s_v = standard error of the coefficient of variation

Units, r_o : individuals / week ,

a : individuals / week²

The results of the first test are given in Table II which shows mean r_o values for each cluster of brown and green hydra populations. The clusters are with respect to the longevity of populations. In both cases, there is a rank correlation between mean r_o and longevity, which is the expected outcome if r_o is determined by the environment whereas a is independent of the environment. Figures 2 and 3 show the mean trajectories for each cluster of green and brown hydra populations respectively. The correlation between r_o (slopes of tangent lines at $t=0$) and longevity (X-intercepts) can also be observed in these figures.

TABLE II: BROWN AND GREEN HYDRA POPULATIONS CLUSTERED BY LONGEVITY

Cluster	Brown Hydra			Green Hydra		
	No. of pop.s	Longevity (weeks)	Mean r_o	No. of pop.s	Longevity (weeks)	Mean r_o
1	3	5	-0.0016	19	>11	0.2858
2	38	4	-0.0805	20	9 - 10	0.2577
3	43	3	-0.1255	33	7 - 8	0.1077
4	17	2	-0.5428	26	5 - 6	-0.0140

Table III describes the distribution of MS_{res} for the three cases described above, for brown and green hydra. For both types of hydra, the second case, i.e., fitting only r_o 's to the trajectories, with a constant a, results in a median MS_{res} which is not significantly different from that of the first case, i.e., fitting both r_o and a to each trajectory separately. On the other hand, using a constant r_o in the

model (the third case) results in a significantly higher MS_{res} . In other words, we can not reject the null hypothesis that holding a constant does not change the median MS_{res} , whereas we can reject the corresponding null hypothesis for holding r_0 constant. These results show that constant a described the population trajectories as well as separate a -estimates for each trajectory.

TABLE III: RESIDUAL MEAN SQUARE (MS_{res}) DISTRIBUTIONS

<u>A. Brown Hydra</u>			
Parameters fitted	Median MS_{res}	st. err. of median	t_s^1
(i) a and r for each population	1.783	0.268	--
(ii) r for each pop.	1.914	0.263	0.35 ns
(iii) a for each pop.	2.676	0.315	2.16 *
<u>B. Green Hydra</u>			
Parameters fitted	Median MS_{res}	st. err. of median	t_s^1
(i) a and r for each population	1.647	0.316	--
(ii) r for each pop.	2.777	3.305	0.34 ns
(iii) a for each pop. ($r = 0.1406$)	11.444	2.558	3.80 ***

¹Sample t - value for the null hypotheses that the median MS_{res} of (ii) and (iii) are not different than MS_{res} of (i).

ns: non-significant; $P > 0.50$

* : $P < 0.05$

*** : $P < 0.001$

4. CONSEQUENCES FOR ECOLOGICAL EQUILIBRIA

So far, the main focus of our discussion was to demonstrate the plausibility of the hypothesis that the rate of change of growth rate, a , is constant for a population in an environment without food. It was shown that, contrary to the predictions of simplistic rate-based models, the decline of a population in an environment without food does not happen at a constant relative rate, and the rate of change of the decay rate, a , is plausibly a constant characteristic of the species and independent of the environment in which the decline takes place. A decline with a constant deceleration is, therefore, a better description of the process than assuming a constant death rate.

Let us now turn to the discussion of ecological equilibria. Assuming the absence of all limiting factors besides food supply means that $F(S,N) = F(S/N)$. Equation (3) then takes the following form:

$$\frac{d^2}{dt^2} \ln N = \frac{1}{I} F(S/N).$$

For the growth rate not far from zero, the approximate expression is

$$\frac{1}{I} F(S,N) \cong -a + f\left(\frac{S}{N}\right) = 0$$

where $f(0) = 0$. For an equilibrium we therefore obtain

$$-a + f\left(\frac{S}{N}\right) = 0 \quad (7)$$

There are a number of predictions following the model (3) and its equilibrium form (7).

- (i) Equilibrium population size is proportional to the food supply.

This seemingly obvious statement is not a property of many classical rate-based models in spite of being repeatedly confirmed in the laboratory studies as well as observed in nature. Two examples of experimental and field discussed below favor such proportionality.

First, it was shown that the average density of experimental populations of *Daphnia* is a linear function of the rate of the food (algae) supply (Slobodkin 1954, Murdoch & McCauley 1985). This means that the population size of *Daphnia* to the population size of algae is constant although the population sizes may be at a higher or lower level, depending on rate of supply of algae and on environmental conditions. Other laboratory examples include brown hydra (Slobodkin, 1964), flour beetles (Chapman, 1928) and blowflies (Nicholson, 1954). Most laboratory population studies have not been conducted for a sufficiently long time to reach a zero-growth steady rate (see discussion in Hutchinson, 1978), which we would need to evaluate equilibrium ratios.

Second, Ricklefs, (1979, p. 623) reports data on the populations and biomass ratios of a number of prey species to wolf populations, compiled from various sources. He concludes that despite the differences in prey species and density of prey populations among localities, "the population and particularly biomass ratios ... are amazingly constant."

- (ii) Balanced (equilibrium) ratio of prey population to the predator population and the oscillation frequency of the prey-predator system are independent of the initial growth rates. This result is a consequence of the second-order dynamics incorporated into our model, which does not explicitly contain growth rates in its

equilibrium equation. In a prey-predator system, the growth rate of the prey can be manipulated by changing the amount of its food. In a series of chemostat experiments carried out by Fredrickson and his colleagues, the flow rate of glucose (food supply for bacteria) through the chemostat was changed and the effects on the bacteria (prey) - protozoa (predator) system were reported (Tsuchiya et al. 1972). When the flow rate was reduced twice and four times between three experiments, neither the frequency of the oscillations nor the equilibrium ratio changed significantly, although the amplitude of the oscillations were higher for higher flow rates. This is consistent with the proposed model and in contradiction with the predictions of the rate-based models. Traditional rate-based models contain r 's explicitly in their equilibrium form, thus they are always r -dependent.

- (iii) Oscillations are possible even with a constant food supply (constant prey population size); their amplitude depend on initial growth rates.

Clearly, a second-order model as the simplest expression of delayed dynamics (Ginzburg, 1986) makes oscillations possible even when the food supply is constant. Experimental work by Murdoch & McCauley (1985) and several field studies reviewed by McCauley and Murdoch (1987) clearly demonstrates that *Daphnia* populations can show oscillation even when their food supply (algae) is constant. Oscillations have been observed with a constant food supply and with an initially population size at the equilibrium, which was measured in prior experiments (Slobodkin, 1964). In other words, balanced initial growth rates, in addition to balanced initial population sizes, seem to be necessary conditions for a stable and constant equilibrium.

- (iv) For two "similar" species utilizing the same food, the equilibrium population sizes will be inversely proportional to their acceleration constants in the absence of food.

Assuming f to be the same and linear function for two species utilizing the same food supply, the equilibrium Eq. (10) will give equilibrium population sizes inversely proportional to the species-specific constant a . In our experiments, mean a for brown hydra is 2.8 times higher than that for green hydra. This result is consistent with the proposed model, since a brown hydra population needs approximately 3 times more food, to stay at a constant size, than a green hydra population of the same size (Slobodkin, 1964).

In summary, the proposed approach, however imperfect, is a definite improvement in comparison to the traditional rate-based models. Continuing accumulation of evidence about the dependence or independence of ecological equilibria and oscillation frequencies on Malthusian parameters of the interacting species will judge the validity and generality of the proposed view.

ACKNOWLEDGEMENTS

This is contribution number 642 of the Graduate Program in Ecology and Evolution at SUNY, Stony Brook. The experimental data was collected as part of research projects funded by the NSF (grant #BRS83-15184), the Andrew Mellon Foundation, and the Hudson River Foundation.

REFERENCES

- BEDDINGTON, J.R., C.A. FREE, J.H. LAWTON. 1976. "Concepts of stability and resilience in predator-prey models". J. Anim. Ecol. 45:791-816
- BEDDINGTON, J.R., M.P. HASSELL, J.H. LAWTON. 1976. "The components of arthropod predation. II. The predator rate of increase". J. Anim. Ecol. 45:165-185
- CHAPMAN, R.N. 1928. Animal Ecology. New York: McGraw-Hill
- GINZBURG, L.R. 1986. "The theory of population dynamics: I. Back to first principles". J. Theor. Biol. 122:385-399
- HUTCHINSON, G.E. 1978. An Introduction to Population Biology. New Haven: Yale Univ. Press
- McCAULEY, E. and W.W. MURDOCH. 1987. "Cyclic and stable populations: Plankton as paradigm". Amer. Natur. 129:97-121
- MURDOCH, W.W. and E. McCAULEY. 1985. "Three distinct types of dynamic behaviour shown by a single planktonic system". Nature 316:628-630
- NICHOLSON, A.J. 1955. "An outline of the dynamics of animal populations". Austr. J. Zool. 2:9-65
- RICKLEFS, R.E. 1979. Ecology. 2nd edition. New York: Chiron Press
- SLOBODKIN, L.B. 1954. "Population dynamics in *Daphnia obtusa* Kurz". Ecol. Monogr. 24:69-88
- SLOBODKIN, L.B. 1961. Growth and Regulation of Animal Populations. New York: Holt, Rinehart and Winston.
- SLOBODKIN, L.B. 1964. "Experimental populations of hydrida". J. Anim. Ecol. 33(Suppl.):131-148
- SMITH, F.N. 1954. "Quantitative aspects of population growth", Dynamics of Growth Processes, E. Boell (ed.) Princeton Univ. Press.
- TSUCHIYA, H.M., J.F. DRAKE, J.L. JOST, A.G. FREDRICKSON. 1972. "Predator-prey interactions of *Dictyostelium discoideum* and *Escherichia coli* in continuous culture". J. Bacteriol. 110:1147-1153.