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θ -Selection*

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ABSTRACT

Using a generalized form of the logistic equation, $dN/dt = rN[1 - (N/K)\theta]$, where θ permits the inflection point of the growth curve to vary between K/e and K , it is shown that, under certain conditions, there are evolutionary optima for the value of θ . All other things equal, a high value of θ is favored. If there is a maximum on the absolute growth rate, the optimal value of θ is high in a stable environment and low in an unstable environment.

It has been fashionable to divide population growth curves—plots of dN/dt versus N —into two types: r and K . The former curve is relatively high and narrow, the latter low and broad [3]. Yet this dichotomy leaves out fundamental degrees of freedom of the growth curve. Gilpin and Ayala [1] have empirically demonstrated that *Drosophila* growth curves follow a generalized logistic equation:

$$\frac{dN}{dt} = rN \left[1 - \left(\frac{N}{K} \right)^\theta \right], \quad (1)$$

an equation which was first written down by Verhulst [5]. N is population density, r is the low density rate of growth, K is the saturation density (carrying capacity), and θ is the asymmetry of the growth curve.

When $\theta = 1$, the equation is the normal logistic and the growth curve is symmetrical about $N = K/2$. For θ less than 1, the maximum growth occurs for N less than $K/2$ but greater than K/e , where e is the base of natural

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logarithms (see Appendix). This lower bound on the maximum rate of growth may at first seem artificial. It may, however, be a strength of the model, for it would be biologically absurd if the maximum growth occurred at $N=0$. For θ greater than 1, the maximum growth occurs between $K/2$ and K . Further analysis of this model is carried out in the Appendix.

The biological meaning of θ may be seen another way. The relative per capita growth limitation that an additional (or, in economic terminology, marginal) individual has is

$$\frac{\partial}{\partial N} \left(\frac{1}{N} \frac{dN}{dt} \right).$$

For $\theta=1$, the logistic case, this is $-1/K$. That is, each individual has the same effect on the per capita growth rate, regardless of the density at which it is added. In general, this per capita growth limitation is

$$-\frac{\theta}{N} \left(\frac{N}{K} \right)^\theta$$

This relationship is plotted as a function of N for different values of θ in Fig. 1. For $\theta < 1$, individuals introduced earlier (i.e., at low densities) have much greater growth limitation than individuals introduced later. For $\theta > 1$, individuals introduced later have greater growth limitation.

The different parameter values of θ have different underlying biological mechanisms. The logistic case, $\theta=1$, could correspond to cases where homogeneous resources are supplied to the system at a constant rate, or to cases where the effect of interference between individuals is additive. The case $\theta > 1$ could correspond to a territorial system in which there is no

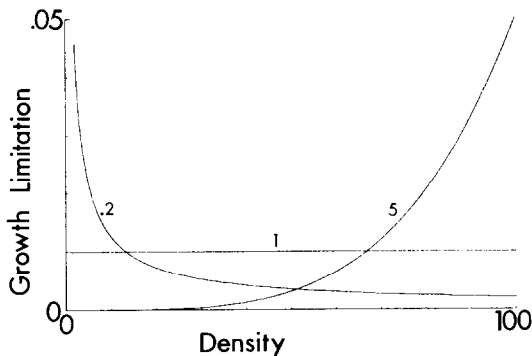


FIG. 1. Relative per capita growth limitation versus density for values of $\theta=0.2$, 1, and 5. K is taken as 100. Note that the integral under all three curves is 1.

growth limitation until all of the individual territories are filled. The case $\theta < 1$ could correspond to a situation of resource heterogeneity in which the first individuals exhaust the quality resources, or to cases where interference is perceived in a nonlinear fashion such that the affect of interference from a few individuals is as serious as interference from many individuals, as might be the case with certain metabolic waste products.

In the following we will analyze the growth strategies involving intraspecific differences between r , K and θ . For simplicity, we must assume no interaction between strains or genotypes. A genotype or strain will only interact with the total population density, N .

r -selection occurs in the absence of competition and other forms of density-dependent growth regulations. It may be said to occur in unsaturated environments. The population grows exponentially (positive or negative). Genotypes with higher r are favored by natural selection. This increases the average r of the entire population.

K -selection connotes selection under density-dependent population regulation, where the population density is at or near a steady state. It may be said to occur in saturated environments. K -selection is for improved competitive ability. This may involve increased effectiveness in the exploitation of resources, defined to be the ability of the population to subsist at the lowest possible resource densities. Or it may involve interference; either the ability to interfere with a competitor, or the ability to escape the pre-existing interference of a competitor.

It is important to understand that K -selection is not correlated with changes of K , the single species equilibrium population density. Failure to realize this has led to much confusion in the literature. First, increased exploitation effectiveness, defined above, can either increase or decrease the equilibrium density K of a consumer population: K will decrease if the exploitation population is beyond the optimal harvesting rate of its renewable resources, and will increase otherwise [2]. An example where selection for increased exploitation effectiveness reduces K is shown in Fig. 2. Two haploid strains of a consumer population compete for a single (logistically) renewable resource; the superior competitor overexploits the resource and thus comes to equilibrium at a lower density. Second, interference may also lower K . Any form of intraspecific aggression wastes energy that could otherwise be used for reproduction; this would likely reduce equilibrium densities. Poisoning would behave the same way. And territoriality in which extra resources were claimed would clearly lower K .

It is thus rather obvious that selection should favor different growth strategies in saturated and unsaturated environments. More interesting strategic possibilities occur in partially saturated environments, wherein a population is periodically disturbed below its equilibrium density (its K) and must grow back to this steady state.

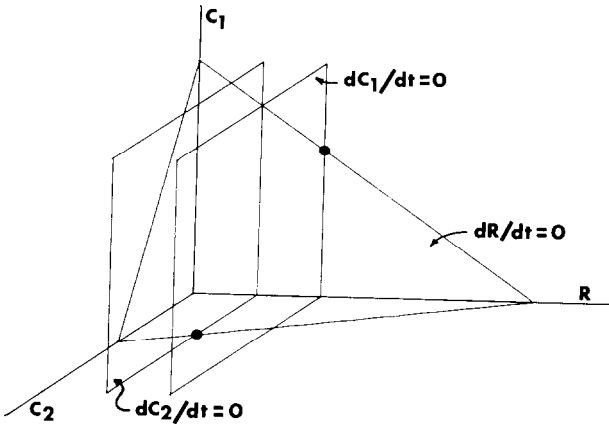


FIG. 2. Hypothetical instance of exploitation of a renewable resource (R) by two genetic strains of a haploid species, whose densities are denoted by C_1 and C_2 . The zero growth planes for each of the two genetic strains and for the resource are drawn. C_2 can reduce the resource below the density required for C_1 's continued survival; thus, the C_2 strain will exclude C_1 . But the equilibrium density of a pure strain of C_2 (the solid circle in the C_2 - R plane where the C_2 and R zero growth planes intersect) is lower than the equilibrium density of a pure C_1 strain. Thus, evolution from C_1 to C_2 reduces the equilibrium density of the species.

Assume that a population whose growth is described by Eq. (1) has been K -selected for a long period of time. All genetic strains in the population would have to have the same K ; that is, their growth curves would have to be zero at $N = K$, where N is the sum of the densities of all of the strains. Differences in r and θ would be neutral. Thus, there could be a variety of genetic strains with growth curves of different height and asymmetry, all of which crossed the N axis at the same point, K [see Fig. 3(a),(c),(e)].

If such a population now enters an evolutionary time regime in which its density is periodically reduced below K , the strains of different r and θ , which had previously been neutral, will be selected. If the population is disturbed to and maintained at a density $N = (1 - D)K$, where D is the percent disturbance, the genetic strain with the highest per capita growth rate will be selected. The K of the various genetic strains will initially remain the same.

The conventional r -selection argument, which assumes θ is fixed at unity, goes as follows. Different genotypes have different growth rates as a function of the total population density, N . When N is reduced below K , the genotypes with the highest $(1/N)dN/dt$ will be selected. This is pictured in Fig. 3(a),(b).

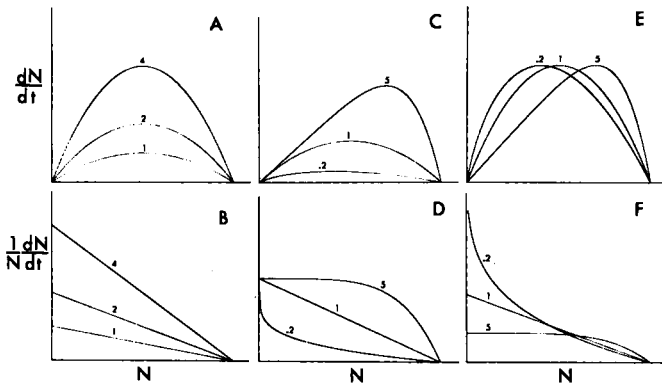


FIG. 3. Population (upper row) and per capita (lower row) growth curves for various instances of Eq. (1). K is fixed in all cases. $\theta = 1$ in (a) and (b); the values of r are labeled. $r = 1$ in (c) and (d); the values of θ are labeled. $(dN/dt)^{\max}$ is constant in (e) and (f); the values of θ are labeled.

With θ free to change, the possibilities expand. There are two limiting cases; r may be fixed, or the maximum dN/dt may be fixed. If r is fixed, the situation is as pictured in Fig. 3(c),(d). Genotypes with the highest θ are selected. That is, genotypes that maintain a high growth rate until very near the population's equilibrium density are selectively favored. These would be genotypes that could maintain their "intrinsic" r as long as there was any free resources.

It is also possible to consider that the maximum dN/dt may be limited. This could occur in "falling fruit" systems, or in systems where the surface area of a resource, not its total density, was the important limiting factor. This situation is as pictured in Fig. 3(e),(f). r is inversely related to θ (see Appendix). As can be seen from Fig. 3(f), the favored genotype depends on the extent to which the population density is disturbed below K . For low disturbances, a high θ is favored. For high disturbances, a low θ , less than 1, is favored. But notice that the spread between the per individual growth curves [Fig. 3(f)] is much greater with large disturbances than with small disturbances. This suggests that even if large disturbances were relatively rare with respect to small disturbances, the "optimal" θ could nonetheless be below 1.

This second line of argument may be supported with a population strategy model. Assume that K and the maximum dN/dt are fixed, and only θ may vary (these three uniquely determine r ; see Appendix). Instead of measuring fitness as the growth rate of a genotype within a population at a particular density, introduce a different measure, a population fitness measure. A population pays a cost, a reduction of fitness, when it is

disturbed below its equilibrium density K . It is more vulnerable to random extinction. It loses genetic variability faster. A competitor species may be able to initiate an invasion. This cost, this reduction in population fitness, may be assumed to be proportional to some power of the difference between the current population density and its potential equilibrium density:

$$\text{Cost} = (N - K)^n. \quad (2)$$

The total cost TC, which is a function of the percent disturbance D a population pays when disturbed from K to $(1 - D)K$, is the integral, over the time it takes the population to return to K , of the cost per unit time:

$$\text{TC}(D) = \int_0^\infty [N(t) - K]^n dt, \quad (3)$$

where

$$N(0) = (1 - D)K. \quad (4)$$

This integral converges; it may be calculated on a digital computer. Figure 4 shows the cost of a disturbance from equilibrium as a function of θ and the degree of the disturbance, D . n was assumed to be 2, but the form of the results of Fig. 4 is quite insensitive to the value of n .

Figure 4 shows two things. First, there is an "optimal" value of θ , defined to the θ that minimizes cost, for a given degree of disturbance. For large disturbances, the optimal value of θ is less than 1; for small disturbances, greater than 1. Second, greater costs are associated with larger disturbances, and these may be more important for determining the optimal θ where D is variable. This population fitness approach is thus in complete agreement with the individual selection approach first outlined.

The concepts of r - and K -selection and strategy engendered many interesting empirical studies. This occurred despite imprecision in the definition of the terms. In fact, it is probable that this occurred exactly because of the fuzzy, metaphorical nature of the definitions. In this paper, we have introduced the mathematically based concept of θ -selection. We believe, however, that θ -selection should be viewed more loosely than in the present context. Asymmetry in population growth curves may have played an important role in evolution. We hope that questions related to this idea will be investigated by experiment and observation.

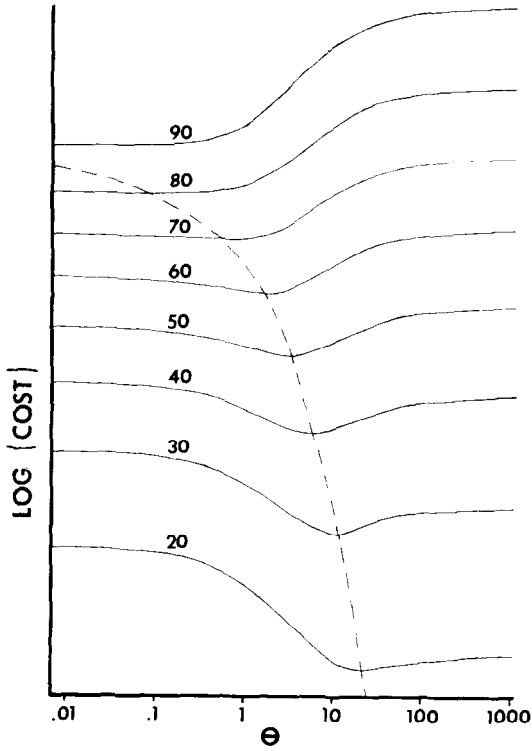


FIG. 4. $\log(\text{cost})$ as a function of θ and D , computed from Eq. (3). The solid lines show cost for a fixed degree of disturbance ($D = \text{up to } 20$). The value of θ that minimizes the cost of a given disturbance is indicated by the dashed line.

APPENDIX

The value of N at which the maximum growth occurs, denoted N^* , for the equation

$$\frac{dN}{dt} = rN \left[1 - \left(\frac{N}{K} \right)^\theta \right] \tag{A1}$$

may be found by taking the partial derivative of this equation with respect to N and setting it equal to zero:

$$\frac{\partial}{\partial N} \left(\frac{dN}{dt} \right) = r - r(1 + \theta) \left(\frac{N^*}{K} \right)^\theta = 0 \tag{A2}$$

This yields

$$N^* = K \left(\frac{1}{1+\theta} \right)^{1/\theta}. \quad (\text{A3})$$

The limiting values as θ approaches 0 and infinity are

$$\lim_{\theta \rightarrow 0} K \left(\frac{1}{1+\theta} \right)^{1/\theta} = \frac{K}{e}, \quad (\text{A4})$$

$$\lim_{\theta \rightarrow \infty} K \left(\frac{1}{1+\theta} \right)^{1/\theta} = K \quad (\text{A5})$$

Substituting N^* into Eq. (A1) gives the maximum growth rate:

$$\left(\frac{dN}{dt} \right)^{\max} = rN^* \left[1 - \left(\frac{N^*}{K} \right)^\theta \right], \quad (\text{A6})$$

which is

$$\left(\frac{dN}{dt} \right)^{\max} = \frac{r\theta K}{1+\theta} \left(\frac{1}{1+\theta} \right)^{1/\theta}. \quad (\text{A7})$$

The limiting values for this as θ approaches 0 and infinity are

$$\lim_{\theta \rightarrow 0} \frac{r\theta K}{1+\theta} \left(\frac{1}{1+\theta} \right)^{1/\theta} = 0, \quad (\text{A8})$$

$$\lim_{\theta \rightarrow \infty} \frac{r\theta K}{1+\theta} \left(\frac{1}{1+\theta} \right)^{1/\theta} = rK. \quad (\text{A9})$$

If the maximum growth rate is fixed and if K and θ are given, Eq. (A7) may be solved for r :

$$r = \left(\frac{dN}{dt} \right)^{\max} \frac{(1+\theta)^{1+\theta}}{\theta K}. \quad (\text{A10})$$

Richards [4] has also analyzed Eq. (A1); he demonstrated that in the limit as θ approaches 0 the equation becomes the Gompertz equation, $dN/dt = rN \ln(K/N)$, which directly explains the result (A4).

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