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Source: *The American Naturalist*, Vol. 104, No. 935 (Jan. - Feb., 1970), pp. 1-24

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: <http://www.jstor.org/stable/2459070>

Accessed: 08-07-2017 20:55 UTC

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# THE AMERICAN NATURALIST

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Vol. 104, No. 935

The American Naturalist

January–February 1970

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## LIFE HISTORICAL CONSEQUENCES OF NATURAL SELECTION

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Living beings show much variation of both genetic and environmental origin in the patterns of their life histories. The case of the two ecological forms of the trout (*Salmo trutta*) may serve to illustrate this variation (Alm 1949, 1959). The lake form of this species (*S. t. lacustris*) lives in a more favorable environment, grows to a bigger size, and matures at the age of 5–7 years. The river form (*S. t. fario*) inhabits a poorer environment, grows to a smaller size, and matures at the age of 3–5 years. When grown under similar conditions the difference in the growth rate of the two forms disappears, but that in the age of maturity does not. In addition, within a population of any one form some individuals grow faster than others and mature at an earlier age, but at about the same or even smaller size than the individuals growing more slowly. The most fruitful approach toward the elucidation of such variation, as in many other biological problems, is to regard it as adaptive, that is, contributing toward the fitness of the organism. Fisher (1958) was one of the first to comment on the problem of the life history strategy, and he presented an analysis of the problem of the sex ratio. Other interesting attempts along these lines are those of Lack (1954) and Cody (1966) on clutch size in birds, Cole (1954) and Lewontin (1965) on the role of life-history parameters in determination of  $r$ , and Istock (1967) on complex life cycles. Williams (1966) and Murphy (1968) also consider many aspects of this problem from this viewpoint. MacArthur and Wilson (1967) summarize the present-day status of the problem.

### MEASURES OF FITNESS

If we are to explain life history patterns as adaptive or fit, we need to define fitness precisely. We must, of course, bear in mind that life-history patterns may not always be “fit,” since fitness may not always increase with time in a fluctuating environment, and all environments are fluctuating. Even the concept of an optimum or fittest genotype may be deceptive, since

the definition of an optimum is as ephemeral as the environment on which it is based. Nevertheless, the concept of a fittest type provides us with a powerful tool and is often the only useful model in dealing with many biological problems; it will be employed here in that spirit.

The Malthusian parameter,  $m$ , and the carrying capacity of the environment,  $k$ , are the two measures of fitness available to us. Fisher (1958) proved that fitness, as defined by  $m$ , will always increase if we assume a fixed degree of inbreeding and a constant environment and disregard the effects of population density. Without assuming a fixed degree of inbreeding, and taking population density explicitly into account, MacArthur (1962) proved that for a stable environment  $k$  will always increase, unless the competing genotypes have different effects on the renewal of the resource.

Consideration of the classical model of population regulation will make clear the interrelation between  $m$  and  $k$ . A population may be largely controlled by factors acting in a density-independent manner, but we believe that this must be accompanied by regulation through factors acting in a density-dependent manner. If we neglect any positive density dependence, then there is a certain population density  $k'$  below which only density-independent factors limit the population growth. As the density increases above  $k'$ , the environment progressively deteriorates. This deterioration may be brought about by an accumulation of metabolites, by the paucity of a resource, or by an intensification of predation. We will consider here models of limitation through a resource or through predation. We will use the degree of satisfaction,  $\psi$ , as an index of the extent to which a resource is limiting. At densities below  $k'$  the resource is not limiting, and the degree of satisfaction equals one. At higher densities the degree of satisfaction will decline toward zero. Both birth and death rates will be depressed with the decline in the degree of satisfaction. If predation is acting as the density-dependent controlling factor, the probability of death through predation will increase with the prey density, while the birth rate is assumed to remain unaffected. With the population density below  $k'$ , the growth rate of the population,  $m$ , is constant at some positive value, and this rate is often termed the intrinsic rate of natural increase,  $r$ . The rate,  $m$ , begins to decline as the population density increases above  $k'$ . In a stable environment the population will stabilize at the density at which  $m$  equals zero. This population density is the carrying capacity of the environment,  $k$  (see fig. 1).

A basic postulate of this investigation is that natural selection will tend to maximize  $m$  in the region of the mean density around which the population is maintained. This is a reasonable assumption only if the population density is taken to be quite stable. The life-historical consequences of natural selection in a variable environment will be examined in a later paper (Gadgil, in preparation). In an environment with recurrent catastrophic mortalities the population may consistently be maintained below  $k'$ , and at these densities selection for  $m$  is equivalent to selection for maximum rate of growth in a nonlimiting environment, the “ $r$ -selection” of Mac-

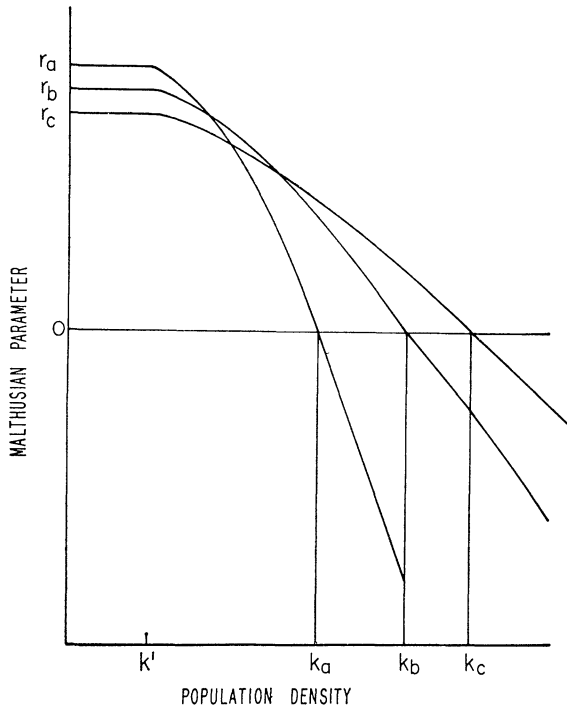


FIG. 1.—Behavior of the Malthusian parameter as a function of population density. The expression  $r_a, r_b, r_c$  is the intrinsic rate of natural increase, and  $k_a, k_b, k_c$  is the carrying capacity of the environment, for the genotypes  $a, b$ , and  $c$ , respectively. The meaning of  $k'$  is explained in the text.

Arthur and Wilson (1967). In a stable environment the population will be maintained close to  $k$ , and since maximizing  $m$  in this case also implies maximizing  $k$ , this will be equivalent to “ $k$ -selection.” Thus  $r$  and  $k$  selection are the two limiting cases of  $m$ -selection at any given density.

Figure 1 compares the behavior of  $m$  as a function of population density for three genotypes,  $a, b$ , and  $c$ . Genotype  $a$  has the highest  $r$ , and  $c$ , the lowest. However, the rate at which  $m$  decreases with increase in population density is different for the three genotypes. This leads to differences in  $k$  of a different order from the differences in  $r$ . Now  $c$  has the highest  $k$ , while  $a$  has the lowest. Therefore, a genotype which is superior in an unlimited environment may be inferior in a limiting one. Genotype  $a$  is the  $r$  strategist, while  $c$  is the  $k$  strategist in the sense of MacArthur and Wilson (1967).

#### PROCESSES OF A LIFE HISTORY

An organism's life history may be looked upon as resultant of three biological processes, namely, maintenance, growth, and reproduction. Any organism has limited resources of time and energy at its disposal. The three component processes of the life history compete for these limited resources.

There are many indications of this. Animals grow little during their active hours when the demands of maintenance are high; much of their growth takes place during the time they are resting. A similar competition between the demands of maintenance and growth is reflected in the seasonal cycles of growth (Needham 1964). Reproduction is a heavy burden which cuts into both physical maintenance and growth. As much as 50% of the production of the perch (*Perca fluviatilis*) is devoted to reproductive tissue (Le Cren 1962). Many animals do not feed properly during their breeding season and expose themselves to certain hazards only during this time. Barnes (1962) showed that the growth rate of the barnacle (*Balanus balanoides*) is sharply reduced during the spawning season. Murdoch (1966) found that, other mortality factors being of equal intensity, the survival of adult female Carabid beetles of the species *Agonum fuliginosum* from near the end of one breeding season to the beginning of the next is inversely proportional to the reproduction in the first breeding season.

We may then set up the problem of life-history strategy as that of optimal allocation of resources among maintenance, growth and reproduction, just as Cody (1966) did as among clutch size, predator avoidance, and competitive ability. But if fitness is being measured entirely in the currency of offspring, the advantage of devoting resources to maintenance and growth is only insofar as this enhances the reproduction at further stages in the life history. Maintenance is essential to enable an organism to survive to these stages. Growth may enhance both survival and reproductive ability. A continuous increase in fecundity with size is well known in fishes where gonads comprise a fairly constant proportion of the body weight. In social mammals the bigger male often has a larger harem.

#### A MODEL OF A LIFE HISTORY

We may now sum up in a more precise manner what seem to us to be the essential processes of a life history, and set up a formal model. Such a formal model is an essential for visualizing the consequences of the life history processes more clearly. A life history is made up of  $n$  discrete ages;  $\alpha_i$  is the probability of survival from age  $i$  to  $i + 1$  for an individual making no reproductive effort at age  $i$ , in a nonlimiting, predator-free environment;  $\delta_i$  is the increment in size from age  $i$  to  $i + 1$  for an individual making no reproductive effort at age  $i$ , in a nonlimiting environment (growth is unaffected by predation);  $w_i$  is the size of an individual at age  $i$  (see Appendix for symbols used).

We denote the reproductive effort of an individual at the age  $i$  by  $\theta_i$ . It may be visualized as the fraction of the total amount of resources of time and energy available to the individual at that age that is devoted to reproduction. Reproductive effort is assumed to take values between zero and one. It affects the life history in the following ways:

$\alpha_i \cdot f_1(\theta_i)$  is the probability of survival from age  $i$  to  $i + 1$  in a non-limiting, predator-free environment for an individual exerting reproduc-

tive effort  $\theta_i$  at age  $i$ ;  $f_1$  is assumed to be a monotonically decreasing function taking values between zero and one.  $\delta_i \cdot f_2(\theta_i)$  is the increment in size from age  $i$  to  $i + 1$  in a nonlimiting environment by an individual exerting reproductive effort  $\theta_i$  at age  $i$ ;  $f_2$  is assumed to be a monotonically decreasing function taking values between zero and one.

$w_i \cdot f_3(\theta_i)$  is the number of offspring produced at age  $i$  in a nonlimiting environment by an individual exerting reproductive effort  $\theta_i$ . We are using size to express the reproductive potential of an individual. This reproductive potential usually will be a complex function of some physical measure of size such as body weight and other factors. The function  $f_3$  is some monotonically increasing function taking values between zero and one.

The degree of satisfaction,  $\psi$ , may be visualized as the fraction of the resources actually available to the individual that is maximally utilizable. It will take values between zero and one. The degree of satisfaction affects the life history in the following ways:

$\alpha_i \cdot f_1(\theta_i) \cdot g_1(\psi_i)$  is the probability of survival in a predator-free environment when the degree of satisfaction at age  $i$  equals  $\psi_i$ ;  $g_1$  is a monotonically increasing function taking values between zero and one.

$\delta_i \cdot f_2(\theta_i) \cdot g_2(\psi_i)$  is the increment in size from age  $i$  to  $i + 1$ , when the degree of satisfaction at age  $i$  equals  $\psi_i$ ;  $g_2$  is a monotonically increasing function taking values between zero and one.

$w_i \cdot f_3(\theta_i) \cdot g_3(\psi_i)$  is the number of offspring produced at age  $i$  when the degree of satisfaction at that age equals  $\psi_i$ ;  $g_3$  is a monotonically increasing function taking values between zero and one.

The probability of escaping death through predation at age  $i$  is denoted by  $\eta_i$ . It is taken to be a joint function of prey density and predator density. For a given  $\eta_i$  the probability of survival from age  $i$  to  $i + 1$  is  $\alpha_i \cdot f_1(\theta_i) \cdot g_1(\psi_i) \cdot \eta_i$ .

The probability of survival from birth to age  $x$ ,  $l_x$ , is then given by:

$$l_x = \prod_0^{x-1} \alpha_i \cdot f_1(\theta_i) \cdot g_1(\psi_i) \cdot \eta_i.$$

The size at age  $x$ ,  $w_x$ , is given by:

$$w_x = w_0 + \sum_0^{x-1} \delta_i \cdot f_2(\theta_i) \cdot g_2(\psi_i).$$

The number of offspring produced at age  $x$ ,  $b_x$ , is given by:  $b_x = w_x \cdot f_3(\theta_x) \cdot g_3(\psi_x)$ .

Substituting the appropriate values of  $l_x$  and  $b_x$  in

$$1 = \sum_0^n e^{-m \cdot x} l_x b_x$$

gives us an implicit equation for  $m$ .

The parameters  $\alpha_i$ ,  $\delta_i$ ,  $w_0$  are to be regarded as biological constraints on

the life history external to the present model, while  $\psi_i$  and  $\eta_i$  specify the environment. Given these, we are interested in determining the optimum life-history strategy characterized by a set of  $\theta_i$  such that  $m$  is maximized. To arrive at the optimal set of  $\theta_i$  is a difficult problem; we do know that the  $\theta_n$  for the last age  $n$  will be one, since there is no advantage to sparing reproductive effort at that point. Fortunately, efficient methods for directly searching for the optimum with the help of an automatic computer are available (Wilde 1964). One of these, Rosenbrock's method for pattern search employing rotation of coordinates, was programmed for the Harvard Time Sharing Computing System. Table 1 is a reproduction of a computer output of the search for optimum  $\theta_1$  and  $\theta_2$  for a three-age life history,  $\theta_3$  being one. The program demands the values of the relevant parameters and, given these, can compute the value of  $m$  for any pair of  $\theta_1$  and  $\theta_2$ . The search begins with some initial guess at  $\theta_1$  and  $\theta_2$ . If any change in either leads to an improvement in  $m$ , further steps are taken in the same direction; if not, the direction of search is reversed. After the progress in one coordinate system has come to an end, the coordinates are rotated in the direction in which progress has been achieved, and the search begins from the best point in the previous pattern. If there is no further progress with the original step size, the step size is reduced and the pattern repeated. The search continues until there is no further progress with even very small steps. This is a fair indication of having arrived at at least a local maximum, and the program quits the search. This is repeated with some other initial guesses, and the highest peak is chosen in case the function has more than one mode. Fortunately, the function is almost always unimodal.

TABLE 1  
THE COMPUTER OUTPUT OF THE SEARCH FOR THE OPTIMUM IN A THREE-AGE  
LIFE HISTORY OF THE REPEATED-REPRODUCER TYPE

$\theta_1$	$\theta_2$	$e^m$
.50 .....	.50	1.315876
.50 .....	.60	1.318602
.50 .....	.80	1.311383
.60 .....	.60	1.271877
.40 .....	.60	1.35683
.20 .....	.60	1.412448
0 .....	.60	1.446578
0 .....	.61	1.447594
0 .....	.63	1.449364
0 .....	.67	1.451841
0 .....	.75	1.452387
0 .....	.91	1.434525
.01 .....	.80	1.448112
0 .....	.70	1.452747
0 .....	.60	1.446578
0 .....	.71	1.452864
0 .....	.73	1.452816
0 .....	.71	1.451411
0 .....	.71	1.452864

NOTE.—See text for details of the model.  $w_0 = 0.01$ ;  $\delta_0 = 1.0$ ;  $\delta_1 = 1.2$ ;  $\delta_2 = 1.44$ ;  $\alpha_0 = 0.95$ ;  $\alpha_1 = 0.95$ ;  $\alpha_2 = 0.6$ ;  $\psi_i = \eta_i = 1$  for all  $i$ .

## NATURE OF THE PROBLEM

One can consider a profit function, a cost function, and a balance function with respect to fitness for reproductive effort,  $\theta_j$ , at any age  $j$ . The profit in fitness for any given  $\theta_j$ ,  $P_j(\theta_j)$ , will be the contribution to fitness of the offspring produced at age  $j$ , by exerting a reproductive effort,  $\theta_j$ . This contribution will depend on the probability of survival to that age,  $l_j$ , and the number of offspring produced,  $b_j$ . The latter depends on size at that age,  $w_j$ , and on  $\theta_j$ . Since  $\theta_j$  affects neither  $l_j$  nor  $w_j$ ,  $P_j$  will be a monotonically increasing function of  $\theta_j$  for any given  $l_j$  and  $w_j$ . It is zero for  $\theta_j = 0$ , since no offspring are produced for no reproductive effort at all, and has its maximum for  $\theta_j = 1$ . It will be higher at all  $\theta_j$ 's with any increase in  $l_j$  and  $w_j$  (see fig. 2). The particular form of the curve would vary for different kinds of organisms. Thus in a species like the Pacific salmon which has to undertake tremendous migrations in order to reproduce at all, initial reproductive effort to produce just one offspring will be high. But the number of offspring produced with any additional effort beyond this initial effort will increase rapidly. Hence, the profit function will be concave. It may have a different form for a different kind of organism.

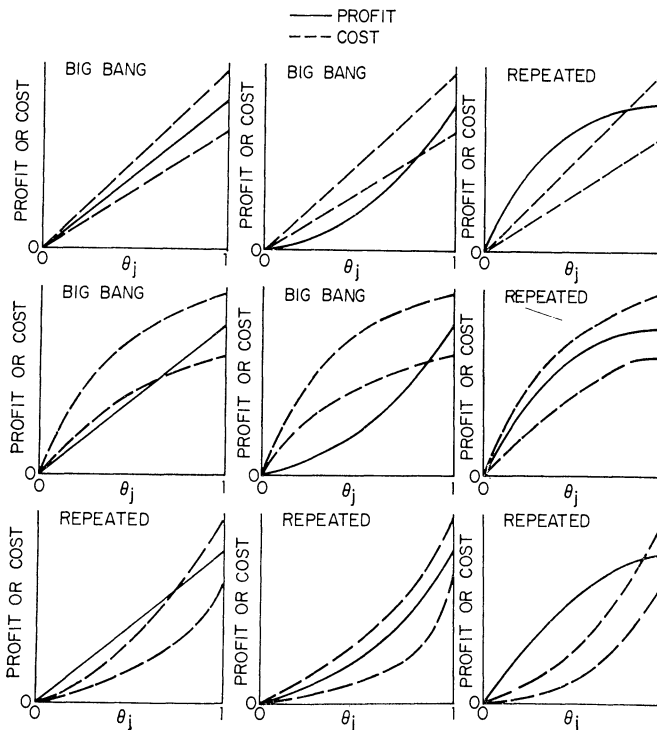


FIG. 2.—Various possible combinations of forms of profit and cost functions for reproductive effort  $\theta_j$  at age  $j$ . The kind of life history to be expected for a given combination is indicated by “big-bang” or “repeated”



The reproductive effort  $\theta_j$  will, however, lower the probabilities of survival to further stages in the life history ( $l_i$  for  $i > j$ ) and decrease the size at these stages ( $w_i$  for  $i > j$ ). Both these effects will reduce the reproductive contribution of ages greater than  $j$ . This is the cost of  $\theta_j$   $C_j(\theta_j)$ . Let the contribution to fitness of all ages  $> j$  be  $F_{j+1}(0)$  when  $\theta_j = 0$ . This will be reduced to zero when  $\theta_j = 1$ , since there would be no survival beyond age  $j$ . The cost when  $\theta_j = 1$ ,  $C_j(1)$  is  $F_{j+1}(0)$  and is zero when  $\theta_j = 0$ , that is,  $C_j(0) = 0$ . The form of the cost function may again vary with the kind of organism. Any improvement in the conditions of existence for ages  $> j$  will lead to an increase in the value of  $C_j(\theta_j)$  for all  $\theta_j$ , and vice versa.

Thus, both the profit and cost increase with  $\theta_j$  and the optimal  $\theta_j$  will be some point of compromise. The form of the profit or cost function has many implications for the nature of this compromise. Let us consider three forms: concave, convex, or linear. An examination of the nine possible combinations shows that unless either (a) the profit function is convex, or (b) the cost function is concave, the balance cannot be at a maximum for any intermediate value of the reproductive effort ( $\theta_j$ ) between zero and one (see fig. 2). If the above condition does not hold, the optimum strategy will be not to reproduce at earlier ages, when the cost will lie above profit of all values of  $\theta_j$ , and then to reproduce to death at some age when the cost will lie below profit and when both will continuously diverge so that the maximum of balance is at  $\theta_j = 1$ .

Other possible forms of profit and cost functions may be considered, for example, an S-shaped form. An inspection of figure 3 will show that for such forms an intermediate value of optimal reproductive effort is possible in the range where the profit or cost function is appropriately concave or convex.

Among the perennial organisms the two strikingly different kinds of life-history strategies are the repeated reproducers, or iteroparous organisms, and the big-bang reproducers, or semelparous organisms. In terms of our model, the repeated reproducers are organisms with a reproductive effort intermediate between zero and one at many ages, and this

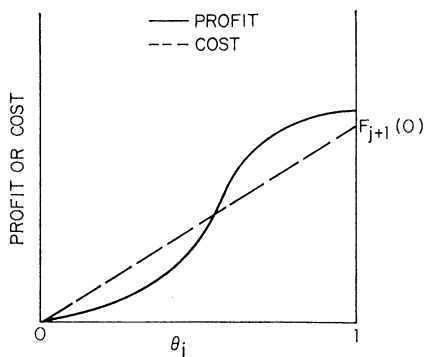


FIG. 3.—Profit and cost functions for reproductive effort  $\theta_j$  at age  $j$ . The expression  $F_{j+1}(0)$  is the contribution to fitness by ages  $> j$  for  $\theta_j = 0$ .

category comprises the majority of perennials. The big-bang reproducers have a reproductive effort of zero for many ages, followed by the suicidal reproductive effort of one. This category includes a few organisms such as the Pacific salmon or the bamboo tree. Our model suggests a possible significance of this difference.

Any improvement in survival or size to an age  $j$  will lead to an increase in the value of the profit  $P_j(\theta_j)$  for all values of  $\theta_j$ . However, such a change will also mean better survival and larger size at ages  $> j$ , and hence an increase in the cost  $C_j(\theta_j)$  for all values of  $\theta_j$  as well. In general, any change in the profit will be reflected in a similar change in cost, though the reverse is not true. The effects of simultaneous changes in profit and cost cannot be considered at this general level.

It is necessary to obtain more precise analytic or numerical results for much of the further exploration of the model. For this purpose it is necessary to specify the forms of the six relationships postulated in the model. Since we have no information on the precise forms of the functions involved, it is appropriate to choose the simplest reasonable forms. However, it is also necessary to make sure that the particular forms of the relationships chosen are not responsible for the results of the model suggested, but rather that the results are general and would hold for any reasonable function. If this is not so, and two reasonable forms for any function give different results, this is of significance and should be explored.

The relationships involved are either monotonically decreasing ( $f_1, f_2$ ) or monotonically increasing ( $f_3, g_1, g_2, g_3$ ). We decided to explore the effect of three possible forms for each of these two kinds of relationships. The forms are linear, concave, and convex. For the monotonically decreasing function we have used:  $f(x) = 1 - x$ ,  $f(x) = (1 - x)^2$ , and  $f(x) = 1 - x^2$ ; and for the monotonically increasing functions we have used:  $f(x) = x$ ,  $f(x) = x^2$ , and  $f(x) = 2x - x^2$ .

We performed a large number of numerical experiments in which the optimal life-history strategies are computed for a wide range of sets of parameters for various combinations of forms of these six functional relationships. The results of these experiments show that under the assumption of any particular form for any of these six relationships the *direction* of a change in the reproductive effort resulting from some change in a particular parameter will always be the same.

We have shown above that either (a) the profit function must be convex or (b) the cost function must be concave for an intermediate reproductive effort between zero and one to be optimal at any age. This result is borne out by an examination of these functional forms. The function  $f_3$ , the increase in the number of offspring produced at any age with an increase in the reproductive effort at any age, corresponds to the profit function. The reduction in the probability of survival ( $f_1$ ) or in the amount of growth ( $f_2$ ) to the next age with an increase in the reproductive effort at any age together constitute the cost function. A convex form of  $f_1$  or  $f_2$  corresponds to the concave form of the cost function, which is essentially of

the form of  $(1 - f_1)$  or  $(1 - f_2)$ . It was found that the convex form of  $f_1$  will suffice to render intermediate reproductive effort optimal, while the convex form of  $f_2$  will not so suffice. It then appears that the influence of reduction in the probability of survival,  $f_1$ , is much greater than that of reduction in growth,  $f_2$ , on determining the form of the cost function.

For further computations, we have selected one set of functions for each of the two kinds of life histories, namely the repeated and big-bang reproducers. Choosing the simplest adequate form in each case, we have for the big-bang case  $f_1(\theta) = 1 - \theta$ ,  $f_2(\theta) = 1 - \theta$ ,  $f_3(\theta) = \theta$ ,  $g_1(\psi) = \psi$ ,  $g_2(\psi) = \psi$ , and  $g_3(\psi) = \psi$ .

Since either  $f_1$  or  $f_3$  must be convex for a repeated reproducer, we choose  $f_3(\theta) = 2\theta - \theta^2$ , leaving the other five functions the same as in the case of big-bang reproducers.

#### BIG-BANG STRATEGY

With the restriction that the reproductive effort  $\theta$  can take values of only zero and one, as is optimal when the profit function is not convex and the cost function is not concave, the problem of optimum strategy for big-bang reproducers reduces to that of choosing the optimal age for reproduction.

Let  $j$  be the age of reproduction, then  $1 = e^{-m_j j} \cdot l_j \cdot b_j$  for  $\theta_i = 0$  for  $1 \leq i \leq j - 1$  and  $\theta_j = 1$ , where  $m_j$  is the Malthusian parameter of the life history, if reproduction occurs at age  $j$ .

Now

$$l_j = \prod_0^{j-1} \alpha_i \cdot \psi_i \cdot \eta_i,$$

$$w_j = w_0 + \sum_0^{j-1} \delta_i \cdot \psi_i,$$

$$b_j = w_j \cdot \psi_j, \text{ and}$$

$$e^{m_j} = (l_j b_j)^{1/j} = \left( \prod_0^{j-1} \alpha_i \psi_i \eta_i \left( w_0 + \sum_0^{j-1} \delta_i \psi_i \right) \psi_j \right)^{1/j}$$

It is this expression, therefore, which must be maximized by an appropriate choice of  $j$ .

Thus if  $w_0 = 0$ ,  $\delta_i = i + 1$ ,  $\alpha_i = 1$ ,  $\psi_i = 1$ ,  $\eta_i = 1$  for all  $i$ , the optimal age of reproduction is 3 years.

#### COLE'S RESULT

In 1954 Cole published a very interesting theoretical paper on the problem of life-history strategy. An oft-quoted result from this study is

the following: "For an annual species (i.e. one that can reach sexual maturity at the age of one), the absolute gain in intrinsic population growth that can be achieved by changing to perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size." Thus increasing the litter size from five to six, or from fifty to fifty-one at age one would serve the same purpose as having a litter of five or fifty every year. From this result we expect maturity never to be postponed and a very high reproductive effort to occur at age one. Contrary to these expectations we found the optimum reproductive effort at age one,  $\theta_1$ , to be zero in our illustration in table 1. The discrepancy is due to one unrealistic assumption in Cole's (1954) treatment. The assumption is that there is no mortality during the course of the life history. Since Cole is concerned with the maximum advantage that can be accrued through changing from the habit of annual to perennial reproduction, the assumption of no mortality beyond age one is quite reasonable. However, the assumption of no mortality in the course of the first year of life is not. In the case of the lapwing (*Vanellus vanellus*), which has a moderate clutch size of four, the mortality during the first year of life is at least twice as high as the adult mortality (Lack 1954). With a larger litter size the mortality is relatively that much higher for the very young stages. If we worry only about the female part of the population, it is reasonable to suppose that, whatever the litter size, just about one female offspring would survive to age 1 in an annual species; that is,  $l_1 \cdot b_1 \sim 1$ . Since litter size is assumed to be constant at all ages, and mortality nil beyond age 1 in Cole's model;  $l_x b_x = l_1 b_1 \sim 1$  for all ages.

Then for an annual species  $1 = e^{-m} \cdot l_1 \cdot b_1$  and  $m = \ln(l_1 \cdot b_1)$ .

For a perennial species

$$1 = \sum_1^{\infty} e^{-m \cdot x} \cdot l_x \cdot b_x = l_1 b_1 \sum_1^{\infty} e^{-m \cdot x}$$

and  $m = \ln(l_1 \cdot b_1 + 1)$ , since  $l_1 \cdot b_1 \sim 1$ ,  $l_1 \cdot b_1 + 1 \sim 2 \cdot l_1 \cdot b_1$ .

We therefore suggest that Cole's result be modified to: *For an annual species the absolute gain in the Malthusian parameter which could be achieved by changing to the perennial reproductive habit would be approximately equivalent to doubling the average litter size.*

This amendment of Cole's result makes it more reasonable that organisms might have life histories involving repeated breeding, that maturity might be postponed under certain circumstances, and that less than maximal effort might be devoted to reproduction on first reaching maturity.

#### CHANGE IN REPRODUCTIVE EFFORT WITH AGE

Should the reproductive effort decrease, stay constant, or increase with age? In the case of big-bang reproducers the answer is that the reproductive effort is constant at zero for a number of ages, finally jumping to one

at the age of suicidal reproduction. In the case of repeated reproducers, however, all we know is that it increases to one at the last age.

The change in the optimal reproductive effort with age depends on the change in the balance of profit and cost of reproductive effort with age. For any given life history, the cost function  $C_j$  will decrease as the age  $j$  increases. This is because the cost is determined by the contribution to fitness of reproductive effort at ages  $> j$ . The number of such ages contributing to  $C_j$  decreases as  $j$  increases; hence, the decrease in  $C_j$ . There will be two opposing effects in determining the change in the profit function  $P_j$  with age. The decrease in the probability of survival to age  $j$  as  $j$  increases and the reduction in the contribution to the fitness by offspring produced at greater age will both tend to reduce  $P_j$  with any increase in  $j$ . On the other hand,  $P_j$  might increase with age  $j$  because the number of offspring produced at any age may increase with a size increase. Since no single complete algebraic result has been obtained with respect to the balance between profit and cost, we have resorted to numerical experiments. In these experiments the optimal reproductive efforts are computed for a wide range of sets of parameters. In every one of the cases we have computed, the *reproductive effort increases with age* (see table 2 and fig. 4). Williams (1966) has arrived at a similar conclusion, though on the basis of a deficient argument which neglects the possibility of decrease in the profit function with age.

There are some data to support the relevance of this result. A measure of reproductive effort in egg-laying fishes is the ratio of ovary weight to body weight. This ratio is known to increase with age in the case of a number of fish, for example, *Hippoglossoides platessoides*, *Melanogrammus aeglefinus*, *Clupea harengus* and *Clupea pallasii* (Gerking 1959).

TABLE 2  
OPTIMUM REPRODUCTIVE EFFORT AT VARIOUS AGES FOR A FIVE-AGE  
LIFE HISTORY OF A REPEATED-REPRODUCER TYPE

	PARAMETER SET NUMBER							
	1	2	3	4	5	6	7	8
$\alpha_0$ .....	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80
$\alpha_3$ .....	0.95	0.60	0.95	0.60	0.95	0.60	0.95	0.60
$\delta_0$ .....	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
$\delta_1$ .....	1.20	1.20	1.20	1.20	0	0	0	0
$\psi_0$ .....	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80
$\psi_4$ .....	1.0	1.00	0.60	0.60	1.00	1.00	0.60	0.60
$\theta_1$ .....	0	0	0	0	0	0.26	0.27	0.30
$\theta_2$ .....	0	0.07	0.09	0.21	0	0.32	0.34	0.42
$\theta_3$ .....	0	0.40	0.45	0.72	0	0.42	0.45	0.68
$\theta_4$ .....	0.18	0.47	0.59	0.75	0.32	0.53	0.55	0.70
$\theta_5$ .....	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

NOTE.—See text for details of the model.  $\alpha_0 = \alpha_1 = \alpha_2$ ;  $\alpha_3 = \alpha_4$ ;  $\delta_i = (\delta_1)^i$  for  $i = 1-4$ ;  $w_0 = 0.01$ ;  $\psi_0 = \psi_1 = \psi_2$ ;  $\psi_4 = \psi_5$ ;  $\eta_i = 1$  for all  $i$ .

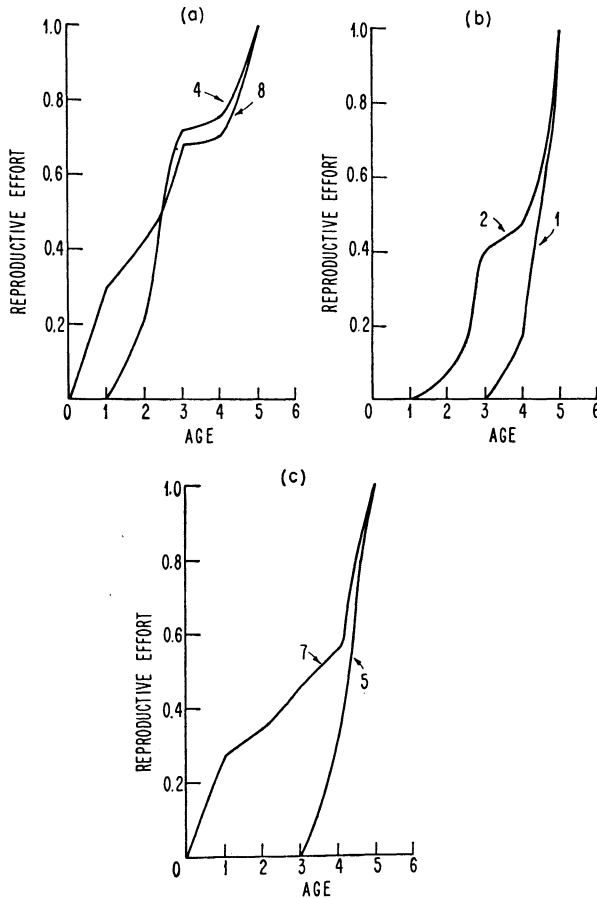


FIG. 4.—Behavior of reproductive effort as a function of age for some of the life histories from table 2. (a) Illustrates the effect of cessation of growth at age 1 in set 8, in comparison with continued growth in set 4. (b) Illustrates the effect of lower probability of survival beyond age 3 in set 2, in comparison with set 1. (c) Illustrates the effect of lower degree of satisfaction beyond age 4 in set 7, in comparison with set 5.

#### EFFECT OF AGE-SPECIFIC CHANGES

Any change in survival or growth to an age  $j$  will lead to a change in the profit function depending on the direction of such a change. This change will also mean a change in survival or size in the same direction at ages greater than  $j$ , and hence a change in the cost function in the same direction as the change in the profit function. On the other hand, changes in growth, survival, or favorability of environment at ages beyond  $j$  are reflected only in the cost function  $C_j$  for age  $j$ , and not in the profit function  $P_j$ . An examination of figure 2 suggests that, holding the profit function constant, any increase in the cost function will lead to a decrease in

the optimal reproductive effort, and vice versa (see table 2 and fig. 4). A similar situation, that is, an increase in cost function while the profit function is held constant, will lead to an increase in the age of reproduction for the big-bang reproducers. If an organism occupies somewhat different niches in different phases of life history, a change in one of the niches in which a succeeding phase of the life history is spent may lead to a situation where the cost function is changed for some ages without a change in the profit function. A detailed consideration of the problems of a multiple-niche life history will be published later (Gadgil, in preparation).

Here we will consider one possible illustration afforded by *Daphnia*, in which subjection to predation only at higher sizes seems to have led to the evolution of forms with high reproductive effort and low growth rates. There are two forms of *Daphnia lumholtzi* in Lake Albert in East Africa (Green 1967): the helmeted form and the *monacha* form. The *monacha* form has a longer carapace and is very susceptible to fish predators of the genus *Alestes*, which feed heavily on *Daphnia* longer than 1,000  $\mu$ . The *monacha* form is abundant in the mid-lake where the predators are absent. In Ndaiga lagoon, adjacent to the lake, where *D. lumholtzi* is subject to fish predation, the slower-growing dwarf helmeted form is much more abundant. The *monacha* form present in this lagoon is also more dwarfed than the mid-lake form. Presumably, the mid-lake *monacha* form is the least adapted, while the helmeted form in the lagoon is the most adapted, to fish predation. The ratio of brood volume to carapace length is lowest in the mid-lake *monacha* form, is intermediate in the *monacha* form in the lagoon, and is highest in the helmeted form in the lagoon (see table 3). Green's (1956) data suggest that for a given strain of *Daphnia* the total brood volume is expected to increase at more than a linear rate with carapace length; that is, their ratio should increase with length under a given set of environmental conditions. The higher ratio at smaller lengths that obtains for the lagoon form could be due to a richer environment of the lagoon, since under better feeding conditions the ratio could be expected to increase. This seems unlikely because Green (1967) presumes that the *monacha* form in the lagoon grows more slowly, and this suggests a poorer environment for the lagoon. The differences, on the other hand, could be genetic rather than environmental. This is rendered plausible by studies

TABLE 3  
TOTAL BROOD VOLUME, MEAN CARAPACE LENGTH, AND THEIR RATIO FOR FORMS  
OF *Daphnia lumholtzi* FROM NDAIGA LAGOON, AND MID-LAKE ALBERT

Locality	Form	Total Brood Volume (Mean) $\times 10^{-4}$ in $\mu^3$	Carapace Length (Mean) in $\mu$	Ratio of TBV:CL $\times 10^{-4}$
Ndaiga .....	helmeted	861	850	1.01
Ndaiga .....	<i>monacha</i>	827	940	0.88
Midlake .....	<i>monacha</i>	902	1270	0.71

NOTE.—Based on samples taken in June. Modified from Green (1967).

of growth rates of several strains of *Daphnia* under controlled laboratory conditions by Hrbacek and Hrbackova-Esslova (1960). They found the highest growth rates in clones living in ponds with smallest fish stock and the lowest growth rates in clones living in ponds with largest fish stocks, both within and between species for a number of water bodies in Europe. These differences were almost certainly genetic. Ndaiga lagoon is relatively isolated from Lake Albert, and the populations of *D. Lumholtzi* may be genetically distinct. If so, these observations are consistent with the behavior of our model. The possible significance of this from the point of view of fisheries is worth pondering. By selectively removing larger fish, we may be exerting pressure for the evolution of early-maturing, dwarf races.

#### GROWTH AND REPRODUCTIVE EFFORT

Size has a number of implications for any organism. In general, as the size increases, the amount of resource necessary for a certain level of maintenance increases. Increased size may also lead to an enhanced ability to exploit resources. It is the balance between the two that should serve to determine the reproductive potential of an organism at any size. The number of offspring produced when the reproductive effort ( $\theta$ ) equals one at any stage with size  $w$ , represented by the symbol  $B(w)$ , may serve as an index of the reproductive potential at that stage. Figure 5 describes this relationship of  $B(w)$  as  $w$ . For some organisms such as trees the reproductive potential may continually increase with size (see fig. 5,a). For others such as birds the reproductive potential may reach a maximum at some size and then decline with any size increase beyond that "optimal" size (see fig. 5,b).

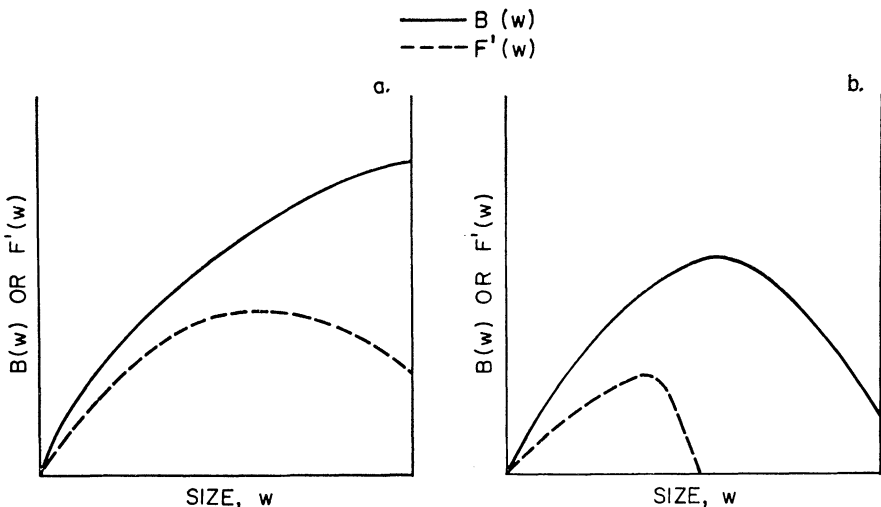


FIG. 5.—Maximum number of offspring produced,  $B(w)$ , and maximum contribution to fitness,  $F'(w)$ , at size  $w$ .



Of as much concern as the reproductive potential is the potential contribution to fitness at any size. The maximal potential contribution to fitness  $F''(w)$ , is the contribution at any size  $w$  of the maximum possible number of offspring produced at the earliest age at which that size is reached. If  $w'$  is the earliest age at which size  $w$  is reached, then  $F''(w) = [l_{w'} B(w)]^{1/w'}$ .

Let us compare  $B(w)$  and  $F''(w)$  for some life history. Because of reduction in survival and reduction in the value of offspring produced at greater ages,  $F''(w)$  will be relatively lower than  $B(w)$  at greater sizes. Therefore, the peak of the  $F''(w)$ -vs- $w$  curve can be at a much lower size (see fig. 5,a); if it rises more sharply the peaks of the two curves will be closer (see fig. 5,b). In other words, if the reproductive potential increases slowly with size, the size of maximal contribution to fitness can be much lower than the size of greatest reproductive potential.

For a big-bang life history, the reproduction will take place at the age and size corresponding to the peak of  $F''(w)$ -vs- $w$  curve. For a repeated-reproducer life history the distribution of reproductive effort and of growth will depend on the shape of the curves, and this has interesting implications for the stage at which sexual maturity is reached, the rate at which reproductive effort increases with age, and the relation between growth and maturity. Inferences regarding these can be derived from essentially two considerations. The first is that growth should continue up to the size at which the reproductive potential,  $B(w)$ , reaches a maximum. The second is that if the curve of  $F''(w)$  vs  $w$  rises sharply beyond any size under consideration, then the cost of reproductive effort will tend to be high relative to profit at that stage, and the optimal reproductive effort will tend to be low. The latter conclusion may be inferred from an examination of figure 2.

Sexual maturity, that is, the stage at which optimal reproductive effort is greater than zero, will not be postponed beyond the size at which the curve  $F''(w)$  vs  $w$  has its peak. This is the size at which any given amount of reproductive effort leads to the greatest contribution to fitness; that is, profit function is very high, and at least some advantage of this will always be taken. This intuitive idea was confirmed through numerical experiments. If the slope of the curve before the peak of  $F''(w)$ -vs- $w$  curve is gentle, the possibility of sexual maturity before the peak is higher. In this case, however, the curve is on the rise and the reproductive effort at earlier ages will tend to be low. This will lead to a rather steep rise in reproductive effort with age. Since maturity has occurred before the  $F''(w)$  peak, which is necessarily at a lower size than the  $B(w)$  peak, growth will continue much beyond maturity. These will be the characteristics of the life history of an organism for which the maximal potential contribution to fitness increases rather slowly with size. Perennial plants and marine fish may exemplify this type. The other type in which this contribution to fitness with size increases rapidly up to a size may be exemplified by birds and mammals. In these the reproductive effort is rather high from

the very beginning, the rate of increase in reproductive effort with age is low, and growth ceases at maturity.

We came to the conclusion above that the organism matures sexually at a size equal to or less than the peak of the  $F'(w)$  curve. This size is necessarily equal to or lower than the peak of the  $B(w)$  curve—the size up to which growth should continue. It might then be expected that *growth will continue beyond maturity or cease with maturity*. If the reproductive potential of an organism existing in any given environment is merely a function of size, there is no reason to expect cessation of growth much before maturity. The rare instances of cessation of growth before maturity, as in the case of the albatross, may be explained by an increase in reproductive potential through learning after the growth has ceased.

#### SURVIVORSHIP AND POPULATION REGULATION

Before considering the effect of survivorship on optimal reproductive effort, we must consider its effect on population regulation. Any increase in the density of predators or density-independent mortality will reduce the value of the Malthusian parameter  $m$  at all population densities (see fig. 6). With such a change the population density at which the Malthusian parameter has a value of zero, that is, the carrying capacity of the environment, is reduced. Thus, the increased incidence of mortality is compensated for by a reduced crowding of the environment.

We have proposed two modes of density-dependent regulation of population. In a completely predator-regulated population, only the death rate increases with population density, while the birth rate remains unaffected. In this situation any increase in predator density or density-independent mortality leading to reduced survival is compensated for by an enhanced

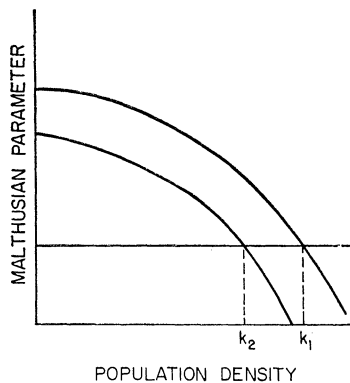


FIG. 6.—Behavior of Malthusian parameter as a function of population density and density-independent mortality. The two curves represent the change in the Malthusian parameter with a change in density-independent mortality, with the lower curve representing the situation under greater mortality.

survival due to reduction in population density. There is thus no net change in life-history parameters. If the population is regulated at least partially by resources, a decrease in the population density is accompanied by an increase in the degree of satisfaction, which affects both birth and death rates. There is here a net change in the life-history parameters at the new level of adjustment of the population.

#### SURVIVORSHIP AND REPRODUCTIVE EFFORT

It would still be of interest to consider the effect of a change in the probability of survival of the same magnitude at all ages on the optimal reproductive effort. Such a change would affect both the profit and cost functions for all the ages in the same direction, and we cannot predict the outcome of such a change analytically except in the case of big-bang reproducers.

For the big-bang reproducers, the age of reproduction  $j$  would be such that

$$e^{mj} = \left( \prod_0^{j-1} \alpha_i \cdot \psi_i \cdot \eta_i \cdot \left( w_0 + \sum_0^{j-1} \delta_i \psi_i \right) \psi_j \right)^{1/j}$$

is maximized. Multiplying the  $\alpha$ 's by some constant  $u$  would mean that now

$$\begin{aligned} e^{mj} &= \left( \prod_0^{j-1} u \cdot \alpha_i \cdot \psi_i \cdot \eta_i \cdot \left( w_0 + \sum_0^{j-1} \delta_i \psi_i \right) \psi_j \right)^{1/j} \\ &= u \left[ \prod_0^{j-1} \alpha_i \cdot \psi_i \cdot \eta_i \left( w_0 + \sum_0^{j-1} \delta_i \psi_i \right) \psi_j \right]^{1/j} \end{aligned}$$

is maximized. This will have no effect on the optimal age of reproduction, since  $u$  does not appear in any part of the expression which is affected by  $j$ . Here both the profit and cost functions have changed by exactly the same magnitude, the relative balance being unchanged. The optimal age of reproduction thus remains the same.

To study the effect of such a change in the case of repeated reproducers, we have examined the behavior of our model in a large number of cases all of which confirmed that, analogous to the result with big-bang reproducers, this change leaves the distribution of optimal reproductive effort with age unchanged. *Thus a change in mortality does not affect the optimal reproductive effort, provided that such a change does not affect the different stages in the life history in a differential manner.*

Williams (1966) equates the profit function for reproductive effort at any age simply with the number of offspring produced, neglecting in particular the effect of probability of survival to that age. An overall change in the probability of survival does not therefore produce a change in his profit function for any age. His cost function, on the other hand,

does depend on the probability of survival beyond the age under consideration. These assumptions lead him to suggest that the optimal reproductive effort will decrease with an overall increase in survival. He further suggests that many oceanic and predatory birds give indications of low reproductive effort at all stages in their life history. This is interpreted as a result of high probability of survival from age to age. This conclusion is inconsistent with our model. An alternative explanation may be that the more stable environments and/or lower incidence of predators allow such birds to exist in more crowded conditions with a lower availability of resources. The next section suggests that optimal reproductive effort at all ages will tend to be low in an environment with low availability of resources.

#### REPRODUCTIVE EFFORT AND AVAILABILITY OF RESOURCES

We may next consider populations at least partially limited by resources. For such populations, not only survival but also growth and birth rates are affected by any change in the degree of satisfaction,  $\psi$ . We are interested here in the effect of a change in the degree of satisfaction which is the same for all ages. This would produce a change in the profit as well as the cost function in the same direction. Hence its effect cannot be predicted analytically, except in the special case of big-bang reproducers.

In the case of big-bang reproducers  $j$  is to be chosen such that

$$e^{mj} = \left( \prod_0^{j-1} \alpha_i \psi_i \eta_i \left( w_0 + \sum_0^{j-1} \delta_i \psi_i \right) \psi_j \right)^{1/j}$$

is maximized. We are interested in the effect of multiplying  $\psi_i$  by some constant  $v$  for all  $i$ .

Then,

$$\begin{aligned} e^{mj} &= \left( \prod_0^{j-1} \alpha_i \cdot \psi_i \cdot v \cdot \eta_i \cdot \left( w_0 + \sum_0^{j-1} \delta_i \cdot \psi_i \cdot v \right) \psi_j \cdot v \right)^{1/j} \\ &= v^{(j+2)/j} \left( \prod_0^{j-1} \alpha_i \psi_i \eta_i \left( w_0/v + \sum_0^{j-1} \delta_i \psi_i \right) \psi_j \right)^{1/j} \end{aligned}$$

is to be maximized. The reproductive potential at birth,  $w_0$ , is negligible in comparison with other terms;  $w_0/v$  will also be negligible unless  $v$  is very small. Very small  $v$  implies an exceedingly deteriorated environment. Since a population cannot be maintained for any length of time in that condition, we can dismiss this case and neglect  $w_0/v$  in the expression. We want to investigate the effects of changes in  $v$  on maximizing the above expression. For the present purpose, all terms except  $v$  are constants for any given age. We therefore want to maximize  $v^{(j+2)/j} c_j$ , where  $c_j$  is the constant factor for age  $j$ . It can be shown that the age  $j$  for which this expression is a

TABLE 4  
CHANGE IN THE OPTIMAL REPRODUCTIVE EFFORT WITH THE DEGREE  
OF SATISFACTION FOR A THREE-AGE LIFE HISTORY OF  
THE REPEATED-REPRODUCER TYPE

	$\psi$							
	.65	.7	.75	.8	.85	.9	.95	1.0
$\theta_1$ .....	0	0	0	0	0	0	0	0
$\theta_2$ .....	0	0.11	0.202	0.278	0.335	0.38	0.43	0.475
$\theta_3$ .....	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

NOTE.—See text for details of the model.  $\alpha_0 = \alpha_1 = \alpha_2 = 0.95$ ;  $\delta_1 = 1.2$ ;  $\delta_2 = 1.44$ ;  $\delta_0 = 1.0$ ;  $\eta_i = 1$  for all  $i$ ;  $\psi = \psi_0 = \psi_1 = \psi_2 = \psi_3$ .

maximum will tend to increase as  $v$  decreases. In other words, *the age for reproduction will tend to increase as the degree of satisfaction or the availability of resources decreases.*

We resorted to numerical experiments to study the effect of the degree of satisfaction on the optimum reproductive effort in the case of repeated reproducers. Table 4 gives the results of one such experiment for different degrees of satisfaction. The optimum reproductive effort increases with the degree of satisfaction. Therefore, analogous to the result for big-bang reproducers, we have: *The optimum level of reproductive effort at all ages increases with the degree of satisfaction for a resource-limited population.*

It was suggested above that in a population at least partially limited by resources, any increase in density-independent mortality, or in predation, would be accompanied by an increase in the degree of satisfaction at which the population can stabilize. The best-adapted strategist under such environmental conditions, that is, the  $k$  strategist, will have a higher optimal reproductive effort (see table 5).

We thus have an interesting picture of the response of life history to mortality. In a population totally controlled by predation any increase in mortality either through increased predator density or through density-independent mortality will lead to the reduction of the population level at saturation. This will bring the death rate down to the previous level, thereby balancing the unchanged birth rate. There will be no selective pressures for changes in the reproductive effort at different ages. On the other hand, if the population is at least partially controlled by resources,

TABLE 5  
OPTIMUM REPRODUCTIVE EFFORT FOR THE  $k$  STRATEGIST AT  
DIFFERENT LEVELS OF DENSITY-INDEPENDENT MORTALITY

	DENSITY-INDEPENDENT MORTALITY				
	0	.1	.2	.3	.35
$\theta_1$ .....	0	0	0	0	0
$\theta_2$ .....	0.278	0.335	0.38	0.43	0.475
$\theta_3$ .....	1.0	1.0	1.0	1.0	1.0

NOTE.—Details of the life history are as in table 4.

the maintenance of the population at a higher degree of satisfaction due to increased mortality will lead to a different set of changes. At this higher degree of satisfaction the birth rate will be increased. The death rate, which was stepped up because of the additional mortality, will be lowered because of this increase in the degree of satisfaction but not quite to the previous level. The slightly increased birth and death rates will balance each other. This will lead to changes in the life-history parameters and hence to selective pressures favoring higher reproductive effort. Such a change will raise the death rate (through  $f_1$ ). It will affect the birth rate in two ways: reduce it through reduction in growth (through  $f_2$ ), and enhance it through increase in proportion of resources devoted to reproduction (through  $f_3$ ). Ultimately, the population will come to an equilibrium at a density higher (and degree of satisfaction lower) than that at which it was maintained before the genetic change, but at a density lower than that at which it was maintained previous to the increase in mortality due to the environmental change.

Organisms vary in the mechanisms of the density-dependent regulation of their populations. In general, the herbivores are more likely to be predator limited, while producers, carnivores, and decomposers are more likely to be resource limited (Hairston et al. 1960). We expect the herbivores to be living in an environment always favorable with respect to resources, and to exhibit a high reproductive effort and life histories with low variation. The producers, carnivores and decomposers may live in conditions of a high or a low availability of resources. Among these, the ones that live in more stable environments with low incidence of catastrophic mortality, as in the "mature" communities of Margalef (1963), will live in environments with relatively low availability of resources. We expect to find low reproductive effort in such organisms. Their life histories will be characterized by late maturation and longer life spans, and their populations will have a greater proportion of older age classes. On the other hand, those living in more variable environments with higher incidence of catastrophic mortality, as in the "immature" communities of Margalef (1963), will have higher quotas of resources available to them. Such organisms would be expected to exhibit high reproductive effort. Their life histories will be characterized by early maturation and shorter life spans, and their populations will show a preponderance of younger age classes. MacArthur and Wilson (1967) have arrived at similar conclusions. Their " $r$  strategists" live in an environment with high availability of resources and show high reproductive effort, whereas their " $k$  strategists," living in an environment with low availability of resources, exhibit low reproductive effort.

#### SUMMARY

The tremendous variation in the life-history patterns of organisms is best explained as adaptive. Any organism has a limited amount of resources at its disposal, and these have to be partitioned between repro-

ductive and nonreproductive activities. A larger share of resources to reproductive activities, that is, a higher reproductive effort at any age, leads to a better reproductive performance at that age; this may be considered as a profit function. This reproductive effort also leads to a reduction in survival and growth and consequent diminution of the reproductive contribution of the succeeding stages in the life history; this may be considered as a cost function. Natural selection would tend to an adjustment of the reproductive effort at every age such that the overall fitness of the life history would be maximized. A model of life history processes has been developed on the basis of these considerations. It leads to the following predictions:

1. If the form of the profit function is convex, or that of the cost function concave, the optimal strategy may be to breed repeatedly. Otherwise, the optimal strategy is to breed only once in a suicidal effort like a salmon (big-bang reproduction).
2. The value of reproductive effort continuously increases with age in the case of repeated reproducers.
3. If all the stages in the life history following a certain age are adversely affected, the age of reproduction will tend to be lowered in the case of big-bang reproducers, and the reproductive effort at all ages preceding that stage will tend to increase in the case of repeated reproducers.
4. As the reproductive potential increases with size at a slower rate, reproductive effort will be lower at maturity, reproductive effort will increase at a higher rate with age, and growth will continue beyond maturity.
5. A uniform change in the probability of survival from one age to the next at all ages would have no effect by itself, on the age of reproduction in big-bang breeders or on the distribution of reproductive effort with age in the repeated reproducers.
6. Such a change in survivorship would lead to a change in the equilibrium density of a population. If the population is resource limited, this would affect the availability of resources to the members of the population in such a way that an increase in mortality would increase the availability of the resources.
7. For a resource-limited organism a greater availability of resources would lead to a lowering of the age of reproduction in the case of the big-bang breeders, and to a greater reproductive effort at all ages for the repeated breeders.

#### ACKNOWLEDGMENTS

We would like to thank R. Baird and T. Schoener for reading the manuscript and making many useful suggestions. This research was supported by National Science Foundation grant 3167 to the Committee on Evolu-

tionary Biology at Harvard and by a grant from the William F. Milton Fund to G. W. Mead.

## APPENDIX

## SYMBOLS USED

$\alpha_i$	= the maximal probability of survival from age $i$ to $i + 1$ .
$\delta_i$	= the maximal possible increment in size from age $i$ to $i + 1$ .
$\eta_i$	= the probability of escaping death through predation at age $i$ .
$\theta_i$	= the reproductive effort at age $i$ , that is, the fraction of the resources available that is devoted to reproductive activities.
$\varphi_i$	= the degree of satisfaction at age $i$ , that is, the fraction of resources maximally utilizable by an individual that is actually available to it.
$a, b, c$	= genotypes representing various alternative life-history strategies.
$B(w)$	= maximal number of offspring that can be produced at size $w$ .
$b_x$	= the number of offspring produced at age $x$ .
$C_j(\theta_j)$	= cost in terms of fitness for a given $\theta_j$ at age $j$ .
$c_j$	= the term remaining after factoring out $v$ from the expression for $e^{m_j}$ for a big-bang breeder.
$e$	= the base of the natural logarithm.
$F_{j+1}(\theta_j)$	= contribution to fitness by all ages $> j$ given a $\theta_j$ at age $j$ .
$F'(w)$	= maximal possible contribution to fitness by the organism at size $w$ .
$f_1$	= function relating survival to $\theta$ .
$f_2$	= function relating growth to $\theta$ .
$f_3$	= function relating birth rate to $\theta$ .
$g_1$	= function relating survival to $\psi$ .
$g_2$	= function relating growth to $\psi$ .
$g_3$	= function relating birth rate to $\psi$ .
$k$	= the carrying capacity of the environment.
$k_i$	= the carrying capacity of the environment for the strategist $i$ .
$k_{ij}$	= $k_i$ at the level of density-independent mortality $j$ .
$k'$	= population density above which negatively density-dependent factors begin to affect.
$l_x$	= probability of survival from birth to age $x$ .
$m$	= the Malthusian parameter.
$m_j$	= Malthusian parameter of the life history for a big-bang breeder when $j$ is the age of reproduction.
$P_j(\theta_j)$	= profit in terms of fitness for a given $\theta_j$ at age $j$ .
$r$	= Malthusian parameter in a nonlimiting environment, or the intrinsic rate of natural increase.
$w_0$	= size at birth.
$w_x$	= size at age $x$ .

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