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ON BREEDING MORE THAN ONCE

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Natural selection is the inevitable consequence of inherited differences in fitness. The fitness of a character is most adequately defined by its effect on the exponential rate of increase, r, whose properties are discussed below; selection will favor any heritable change which tends to increase r (see Charlesworth 1973). In recent years, several attempts have been made to apply the mathematical theory of natural selection to life history phenomena, following the classic work of Cole (1954). Individuals following different life histories can have different fitnesses, and life histories tend to evolve whenever there is heritable variation in the timing of gene effect. I here attempt to analyze some of the problems faced by animals which breed more than once during their lifetimes.

The existence of differences in fitness between alternative life histories may be expressed in one of two ways: as a ratio of fitnesses or as the factor by which a given parameter must be changed in one of the life histories in order to make them of equal fitness. I shall use f to refer to the ratio of finite rates of increase: $f = e^{r_1}/e^{r_2}$ $(r_1 > r_2)$, and k to refer to the factor by which fecundity must be increased in the less fit life history, in order that both life histories will have the same fitness: $k = b_2/b_1$ $(r_1 = r_2)$. Thus, f and k take values of unity when the two life histories being compared are equivalent with respect to fitness or to fitness and fecundity, by definition.

Algebraic symbols are defined in the text whenever a new concept is introduced; the most important are listed in table 1, where they may be compared with those used by previous authors.

COLE'S RESULT

L. C. Cole (1954) attempted to discover how great an increase in fitness is caused by breeding more than once. To do this, he specified a particular population model and then calculated the difference in the rate of increase r that would be caused by changing from a semelparous life history (breeding only once) to an iteroparous mode of life (breeding repeatedly). The main features of his population model were that the population age structure was assumed to be constant and that there was no mortality at any time during life, except that semelparous animals died immediately after breeding.

The intrinsic rate of natural increase, r, as originally defined by Lotka (1907),

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TABLE 1

Definition of Symbols Used in Text

\mathbf{Symbol}	$\operatorname{Concept}$	(1)	(2)	(3)	(4)
N	Population number	Р		N	
r	Intrinsic rate of natural increase of population	~			
e r		r e ^r	m	•••	r
x	Finite rate of increase of population Age; refers the value of a parameter			λ	λ
	to animals of a particular age Time; refers the value of a parameter	x or z	x or i	x	x
$x(x) \dots$	to a particular time Age frequency; frequency of animals				
$b(x) \ldots$	age x Age-specific fecundity; mean number of female zygotes produced per female	c _x			
B	age x in a single reproductive attempt Birth rate; total number of newborn animals produced by a population in	<i>b</i> _{<i>x</i>}	<i>b</i> _{<i>x</i>}	В	m_x
(x)	one period of time Age-specific survival; fraction of all those animals born in a given cycle	B			•••
$p(x) \ldots$	still alive at age x Age-specific rate of survival; fraction of all those animals age x which	l_x	l_x	l_x	l_x
$\iota(x)$	survive to age $(x + 1)$ Age-specific rate of mortality; fraction of all those animals age x dying		αι		
$(a) \ldots \ldots$	before age $(x + 1)$ Fraction of animals born in a given	•••			q
	cycle alive at age a	l_a		C(K)	l_a
•	Rate of survival during first year of life Mean rate of annual survival of im-			с	
0	mature animals Mean annual rate of survival of mature		•••		С
	animals	•••	•••	p	p_{s}
	Age at first reproduction (maturity)	α		K	a
v	a) Age at last reproductionb) Longevity; age beyond which sur-	w			
n	vival is 0 Natural logarithm	λ	•••		

SOURCE.—Col. 1, Cole 1954; col. 2, Gadgil and Bossert 1970; col. 3, Charnov and Schaffer 1973; col. 4, Goodman 1974.

is the infinitesimal rate of increase of a population with stable age structure in an unlimited environment: it is the single real positive root of the equation:

$$1 = \int_{0}^{x=w} e^{-rx} l(x)b(x) \, dx, \qquad (1)$$

where l(x) is the rate of survival to age x, and b(x) is the number of female eggs produced per female age x; w is the longevity, which can be taken to be infinitely great without loss of generality. Although this equation was first derived for a population in an unlimited environment, it is valid for any population with stable age structure. The usage of r was confused by Birch (e.g., Andrewartha and Birch 1954, p. 33), who used it to denote the actual rate of increase of a population in any environment, whether or not the population age structure was stable:

$$dN/dt = rN. (2)$$

These two usages are of course equivalent in the case of a population with stable age structure. Lotka's usage has priority and is mathematically more tractable; Birch's usage, since it deals with achieved rates of increases, has more general validity in fitness equations. In the absence of nomenclature to distinguish between the two usages, I use r to denote the rate of increase defined by equation (1) and r(t) to denote that defined by equation (2). The corresponding finite rates of increase will be written e^r and $e^r(t)$.

By manipulating equation (1), Cole was able to obtain the remarkable result that, "for an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size" (Cole 1954, p. 119). As Cole remarks, this result "arouses some curiosity as to why iteroparity exists at all." He was able to produce a partial solution to this problem by showing that for species which are not necessarily annual, k = $e^{r}/(e^{r}-1)$ (1954, eq. [25]). In Cole's population model, the value of r depends on fecundity (b) and the age at maturity (a) only. By solving this equation for various combinations of these two parameters, Cole was able to show that the advantage of iteroparity (insofar as this is measured by k) is increased as the age at first reproduction is delayed (1954, figs. 2 and 3). But his result for annual species remained at variance with observation until Gadgil and Bossert (1970) published a short analysis of the problem. They maintained that Cole's assumption that there is no prereproductive mortality is unreasonable. Because they wished to calculate the greatest possible advantage of iteroparity, it was considered legitimate to retain the assumption that there is no postreproductive mortality, but they fixed the average rate of prereproductive mortality at a value just sufficient to maintain population number around some constant value. They were then able to obtain the much more plausible result that, "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 equal to doubling the average litter size" (p. 11). Their argument was further refined by Charnov and Schaffer (1973), who showed that when some degree of adult mortality was admitted, the condition for k = 1 was the addition of p/s individuals to the semelparous litter, where p is the rate of postreproductive and s the rate of prereproductive survival. The multiplicative form of Cole's result was amended both by Charnov and Schaffer and by Goodman (1974), who found that $k = e^{r}/(e^{r} - p)$, Cole's original result being the special case in which p = 1.

I shall now show that these arguments are special cases of a quite general set of equations. I shall consider an iteroparous population with fixed life history parameters which determine its rate of increase. An imaginary semelparous population has the same life history parameters, except that after the first reproductive effort the rate of survival is zero. Without the use of restrictive assumptions, it is required to find the factor by which the litter size of semelparous parents must be raised to cause the rate of increase of the semelparous population to equal that of the iteroparous population.

Consider first the semelparous population. The number of animals alive in any given cycle will comprise the survivors of those born in the previous cycle, and of those which although born previously did not reproduce in the previous cycle:

$$N(t + 1) = B(t)[1 - u(0)] + \sum_{1}^{x = (a - 1)} N(x, t)[1 - u(x)], \qquad (3)$$

when N(t) is the total number of individuals alive at time t; B(t) is the number of newborn animals at time t; u(x) is the rate of mortality between ages x and (x + 1). The census is taken after mortality but before reproduction. The summation on the right-hand side of the equation terminates at x = (a - 1)since u(x) = 1 when $x \ge a$, ex hypothesi. Further:

$$B(t) = b_s N(a, t). \tag{4}$$

In this and in subsequent arguments, the subscripts i and s will refer to the values of a parameter in iteroparity and in semelparity, respectively. Substituting this expression into equation (3) and rewriting the age structure terms so that c(x, t) is the frequency of animals age x in the population at time t:

$$N(t+1) = N(t)c(a, t)b_s[1 - u(0)] + N(t)\sum_{1}^{(a-1)} c(x, t)[1 - u(x)].$$
(5)

The finite rate of increase of the population is thus

$$e^{r_s}(t) = b_s c(a, t) [1 - u(0)] + \sum_{1}^{(a-1)} c(x, t) [1 - u(x)].$$
(6)

Note that since the age structure varies with time, the finite rate of increase is not constant (see, e.g., Charlesworth 1970). Recall that the census is assumed to occur after mortality but before reproduction in each cycle. In the case of an annual species, the right-hand summation of equation (6) vanishes, and since c(a, t) is the only age class in the population at the time of census, we have

$$e^{r_s} = b_s[1 - u(0)]. (7)$$

In this case, the finite rate of increase depends only upon life history parameters which are assumed to be fixed and is therefore independent of time. If there is no mortality at any stage, equations (6) and (7) both reduce to

$$e^{r_s} = b_s. ag{8}$$

Before dealing with the iteroparous population, two minor points must be cleared up. First, because we shall allow fecundity to vary with age, it must be the fecundity at some given age that is compared with semelparous fecundity. The obvious choice is the initial iteroparous fecundity, $b_i(a)$. Second, it will be assumed that there is no postreproductive life—that the last year in which an animal breeds is the year in which it dies. It can easily be verified that this

assumption does not affect the conclusion that will be reached. We can now proceed to give the recurrence relationship for population number in the iteroparous population, in which we must take into account the existence of age classes consisting of mature animals:

$$N(t+1) = B(t)[1-u(0)] + \sum_{1}^{(a-1)} N(x,t)[1-u(x)] + \sum_{a}^{w} N(x,t)[1-u(x)].$$
(9)

The number of births is

$$B(t) = \sum_{a}^{w} (x, t)b_{i}(x).$$
 (10)

Hence:

$$N(t + 1) = N(t)[1 - u(0)] \sum_{a}^{w} c(x, t)b_{i}(x) + N(t) \sum_{1}^{(a-1)} c(x, t)[1 - u(x)] + N(t) \sum_{a}^{w} c(x, t)[1 - u(x)].$$
(11)

....

The finite rate of increase is therefore

$$e^{r_{i}}(t) = [1 - u(0)] \sum_{a}^{w} c(x, t)b_{i}(x) + \sum_{1}^{(a-1)} c(x, t)[1 - u(x)] + \sum_{a}^{w} c(x, t)[1 - u(x)]. \quad (12)$$

Putting s = [1 - u(0)] and rearranging,

$$e^{r_i}(t) = \sum_{a}^{w} c(x, t)[sb_i(x) - u(x) + 1] + \sum_{1}^{(a-1)} c(x, t)[1 - u(x)].$$
(13)

In the case of an annual species, the right-hand summation of the right-hand side vanishes; further, if litter size does not vary with age, we have

$$e^{r_i}(t) = \sum_{1}^{w} c(x, t) [sb_i - u(x) + 1].$$
 (14)

But since the census is taken after mortality and before reproduction,

$$\sum_{1}^{w} c(x, t) = 1.$$

Thus, if the annual rate of survival of adults, p(x) = [1 - u(x)], is a constant, the whole of the bracketed expression on the right-hand side of the equation is a constant; and it reduces to

$$e^{r_i} = (sb_i + p).$$
 (15)

If there is no adult mortality, this becomes

$$e^{r_i} = (sb_i + 1). (16)$$

And if there is no mortality at any stage, it becomes

$$e^{r_i} = (b_i + 1). (17)$$

These arguments can now be used to generate results for any desired set of conditions. In the general case, we can equate the finite rates of increase for semelparous and iteroparous populations given by equations (6) and (13), respectively, to obtain

$$sb_{s}c_{s}(a, t) + \sum_{1}^{(a-1)} c_{s}(x, t)[1 - u(x)] = \sum_{a}^{w} c_{i}(x, t)[sb_{i}(x) + p(x)] + \sum_{1}^{(a-1)} c_{i}(x, t)[1 - u(x)]. \quad (18)$$

Hence:

$$sb_{s}c_{s}(a, t) - sb_{i}(a)c_{i}(a, t) = \sum_{(a+1)}^{w} c_{i}(x, t)[sb_{i}(x) + p(x)] + \sum_{1}^{a} c_{i}(x, t)[1 - u(x)] - \frac{(a-1)}{\sum_{1}^{1}} c_{s}(x, t)[1 - u(x)]. \quad (19)$$

If we denote the right-hand side of this equation by A, then we can obtain

$$k(t) = \frac{b_s}{b_i(a)} = \left[\frac{\{[(A/s)]/[b_i(a)]\} + c_i(a, t)}{c_s(a, t)}\right].$$
 (20)

Except for the assumption that there is no postreproductive life (which changes the limits of summation terms in A), this result is quite general. It will be seen that in general k is not independent of time. In the case of annual species, the denominator in the expression for k disappears, since $c_s(a) = 1$. Constant iteroparous fecundity simply replaces $b_i(x)$ with a constant b_i and allows some rearrangement in A. The general equations generate the special results reported by previous authors, according to the conditions imposed on them. This is shown in table 2.

The general rule expressed by equation (20) shows that k depends largely on the values of s and a, which are regarded as fixed parameters identical in the two populations, and to a lesser extent on other factors which may be variable and which will be different in the two populations. The proportion of animals in the semelparous population which are in the *a*th age class, $c_s(a)$, is diminished by adding more prereproductive age classes to the population, and therefore k increases as a increases. Thus, the evolution of iteroparity is a more likely outcome of selection when maturity is delayed; this result was also obtained by Cole (1954). However, it is likely that the value of s, the rate of survival during the first year of life, is more critical. A reduction in the value of s will reduce $c_s(a)$ in all but annual species and will at the same time act directly to raise the value of the numerator of the expression given in equation (20). Both effects will increase k. Moreover, in the case of a population which is stationary in numbers and which has a stable age structure, it can be shown that k varies inversely with the square of s. For species which are not annual, the rate of prereproductive survival after the first year of life will also appear in the equation for k, which it also influences through its effect on c(a).

Conditions	Previous Authors	Factor by Which Semelparous Litter Size Must Be Increased (k)
l. None	:	$k = \left[\frac{(A s)}{b_i(a)} + c_i(a, t)\right] \Big/ c_s(a, t)$
2. Maturity at age 1	:	where $A = s \sum_{(a+1)}^{w} c_i(x, t) b_i(x) + \sum_{1}^{(w-1)} c_i(x, t) [1 - u(x)] - \sum_{1}^{(a-1)} c_s(x, t) [1 - u(x)]$ $k = \frac{(A/s)}{b_i(a)} + c_i(a, t)$
		where $A = sc_i(a, t) + \bigvee_{\infty}^{n+1} c(x, t)[sb(x) + p(x)]$
3. Maturity at age 1; iteroparous fecundity constant	÷	$k = \left[\frac{(1/s)}{b_i}\sum_{a}^{\infty} c(x,t)p(x)\right] + 1$
 Maturity at age 1; iteroparous fecundity constant; adults survival rate constant 	Charnov and Schaffer 1973	$k = \frac{(p/s)}{b_i} + 1$
 Maturity at age 1; iteroparous feeundity constant; no mor- tality 	Cole 1954	$k = (1/b_i) + 1$
6. Maturity at age 1; iteroparous fecundity constant; no adult mortality; population sta- tionary in numbers	Gadgil and Bossert 1970	$k \sim 2$

TABLE 2 COLE'S RESULT MODIFIED FOR VARIOUS CIRCUMSTANCES The remaining parameter is A, which can be written

$$A = s \sum_{(a+1)}^{w} c_i(x,t) b_i(x) + \sum_{1}^{w-1} c_i(x,t) [1-u(x)] - \sum_{1}^{(a-1)} c_s(x,t) [1-u(x)].$$
(21)

This expression is the difference between the weighted mean age-specific rates of survival (excluding s) in iteroparity and semelparity, respectively, plus the weighted mean age-specific fecundity (excluding $b_i[a]$) in iteroparity multiplied by s.

Thus, the general formulation of Cole's result leads to no very neat generalization. Instead, the argument presented above might be interpreted as follows. The likelihood that iteroparity will evolve in an initially semelparous population may be measured by the factor by which litter size must be increased in order to achieve the same rate of population increase as that implied by a given iteroparous life history. When this factor is low, it is likely that increasing the litter size will be the easier solution; when it is high, iteroparity is likely to evolve. This factor is influenced by all the fixed parameters of the schedules of survival and fecundity and is in addition variable in time. In particular, it will tend to increase and thus make the evolution of iteroparity more likely, if the age at maturity is delayed or if the rate of survival during the first year of life is reduced.

TWO KINDS OF ITEROPARITY

Iteroparity is not a simple phenomenon; some iteroparous animals breed only once in the year, while others reproduce almost continuously. I shall call these two extreme strategies "seasonal" and "continuous" iteroparity, respectively. The relative fitness of the two types can be investigated just like that of semelparity and iteroparity, above.

Consider a seasonal breeder which produces b offspring at one time in every year and a continuous breeder which produces one offspring b times every year. Both mature in year a. The cycle of the seasonal breeder, in terms of which its rate of increase will be calculated, is 1 yr, while that of the continuous breeder is (1/b) yr. Similarly, the age at maturity of the seasonal breeder is a cycles, while that of the continuous breeder is ab cycles. I shall use the same population model as Cole (1954), each individual reproducing indefinitely without mortality.

From the definitions given in the previous paragraph, we can write recurrence equations for population number:

seasonal breeders:
$$N_1(t+1) = e^{r_1}N_1(t)$$

continuous breeders: $N_2(t+1) = e^{r_2b}N_2(t)$. (22)

The subscripts 1 and 2 will be used to denote the value of parameters in seasonal and in continuous breeders, respectively. From equation (1) (see Cole 1954):

$$\begin{aligned}
\mathbf{l} &= e^{-r_1} + b e^{-r_1 a} \\
\mathbf{l} &= e^{-r_2} + e^{-r_2 a b}.
\end{aligned}$$
(23)

Multiplying through by e^{r_1} , e^{r_2} , we obtain

$$e^{r_1} = 1 + be^{-r_1(a-1)}$$

$$e^{r_2} = 1 + e^{-r_2(ab-1)}.$$
(24)

If a seasonal and a continuous breeder which are born at the same time also reproduce at the same time, then at the moment of maturity the seasonal breeder will produce b offspring, while the continuous breeder will produce only one offspring. Since, in general, earlier reproduction makes a greater contribution to fitness than later reproduction, the seasonal breeder will inevitably be the more fit. Conversely, if the continuous breeder matures b cycles before the seasonal breeder, it will be the more fit. These are the two extremes of the general case in which the continuous breeder matures (g) years earlier than the seasonal breeder, where 1 > g > 0. We are now in a position to ask an interesting question: at what value of g does the fitness of the continuous breeder become equal to that of the seasonal breeder?

Substituting g into the lower equation of set (23), we can obtain a general expression for relative fitness:

$$f = \frac{e^{r_2 b}}{e^{r_1}} = \frac{[1 + e^{-r_2 b(a-g)-1}]^b}{1 + b e^{-r_1(a-1)}}.$$
 (24)

Equating this to unity and performing the necessary algebra, we obtain

$$g^* = \frac{\ln \left\{ \left[1 + be^{-r_1(a-1)} \right]^{(1/b)} - 1 \right\} + r_2(ab - 1)}{r_2 b}, \qquad (25)$$

where q^* is the value of g when seasonal and continuous breeding have equal fitness. In general, this must be solved by substituting values of r_1 obtained by iteration from the upper equation of set (23), remembering that $r_{2} = (r_{1}/b)$ when f is set equal to unity. Values of g^* are plotted against litter size b for different ages at maturity in figure 1. It can be seen that continuous breeding is always more likely to evolve in animals with very large litters. Even in latematuring forms, for which the graph of g^* with b always slopes upward, the necessity to mature 6 mo or so earlier may not be very arduous, since it represents only a few percent of prereproductive life. In early-maturing forms, the curve actually slopes downward after a litter size of 20 or so. This implies that the ideal conditions for the evolution of continuous iteroparity are a combination of early maturity and very large litter size. Vertebrate endoparasites are perhaps the best-known example of animals which breed continuously, and are remarkable not only for their early maturity but also for their enormous egg production. Fasciola, for example, reproduces for the first time at the age of about 6 mo and thereafter produces several million eggs every year.

Seasonal and continuous breeding represent two extremes of a continuum; many animals produce offspring seasonally, but do so more than once a year. To make the treatment given above more general we might consider an animal

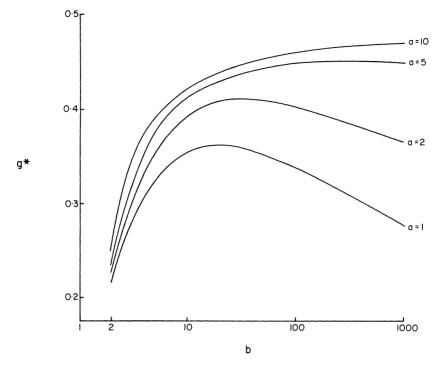


FIG. 1.—Relationship of g^* to litter size b, for different ages at maturity, in strictly continuous iteroparity.

which reproduces n times per year, producing (b/n) offspring on each occasion. By analogy with arguments presented above, we find that

$$g^* = \frac{\ln\left[\left\{\left[1 + be^{-r_1(a-1)}\right]^{(1/n)} - 1\right\}/(b/n)\right] + r_2(an-1)}{r_0 n}.$$

Solutions of this equation are shown in figure 2. It can be seen that g^* varies monotonically with a and b; g^* is larger for any n when a is large and b small.

The arguments presented in this section cannot, of course, be applied straightforwardly to most natural situations. Seasonal breeding is commonly imposed by a seasonal environment, that is, by seasonal fluctuation in the probability of survival of offspring. The conclusions that have been reached, although they will influence events in a seasonal environment, can be tested only in an unvarying environment, and it is to be doubted that any environment is ever constant for very long. Perhaps the nearest approaches are made by the abyssal regions of the sea and by the internal organs of homoiothermic vertebrates. Information concerning the breeding biology of abyssal organisms is scanty. George and Menzies (1967) have claimed that the isopod *Storthyngura* reproduces seasonally, but as Sanders and Hessler (1969) point out, George and Menzies's sample sizes are quite inadequate to bear their conclusion. Sanders and Hessler themselves have much more convincing data, which show that the isopod *Ilyarchna* and the bivalve *Nucula* reproduce almost continuously; on

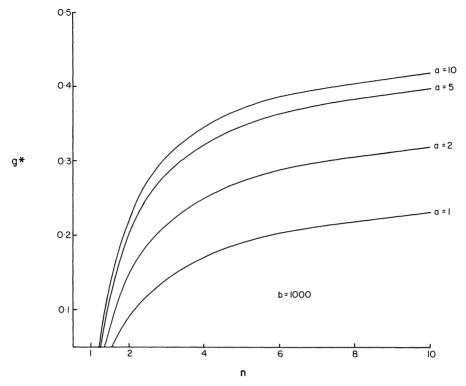


FIG. 2a.—Relationship of g^* to n at different ages at maturity. Calculated for a litter size of b = 1,000.

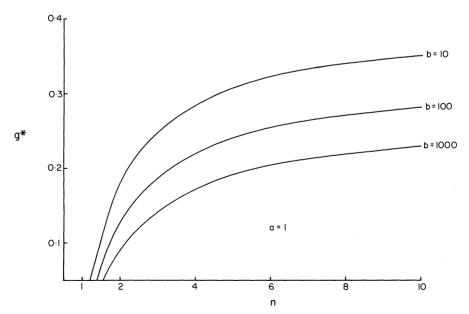


Fig. 2b.—Relationship of g^* to n at different fecundities. Calculated for an annual species.

the other hand, Schoener (1968) shows that reproduction is cyclic in two species of ophiuroid. Unfortunately, nothing appears to be known of the litter size or of the age at maturity in these animals, but at least it seems likely that both seasonal and continuous iteroparity may evolve under conditions where the predictions set out above can be tested. Far more data is available for homoiothermic endoparasites, and it has been pointed out above that these agree with theoretical expectations.

Under what conditions might an animal have two or more breeding seasons in a year, rather than just one? Mature females, or females about to reproduce for the first time, assimilate energy in excess of their requirements for maintenance and growth. This excess energy is used for the maturation of oocytes. It might be shared equally among all the developing oocytes, so that all developed at the same rate; or it might be shared unequally, so that some were ready for oviposition before most had started their development. If all the oocytes could be matured at age a, then half the oocytes could be matured at some age (a - g) if they received all the available excess energy, the other half being matured subsequently in the same year. If g is larger than g^* for the life history of a given animal, selection will tend to favor the adoption of two periods of oviposition rather than one. A possible example of such a process is provided by the work on the smooth newt, Triturus vulgaris (Linn) (Bell and Lawton 1975). Courtship and oviposition occur during the spring, but there are two distinct periods of oviposition, one centered around May 7 and the other around July 14. The difference between the two is thus about g = 68 days. Smooth newts mature at about 4-7 years of age and have a mean litter size of roughly 80-100 female eggs per female (see Bell 1973; Bell and Lawton 1975). The value of g^* calculated for these parameters is about 0.22. Smooth newts in midland England spend about 4 mo of the year in hibernation (Smith 1964), so that about 8 mo remain for feeding and the maturation of oocytes. Thus, we have $g^* = 0.22 \times 8$ mo ~ 55 days. This is consistent with theoretical expectation.

It is not claimed that the above observations constitute a rigorous test of the theory developed in the first part of this section, for the sufficient reason that while the theory is very simple, the animals are not. For example, newts which mature at different times in the year will experience different rates of mortality as adults, changes in the density of larval populations caused by splitting the breeding season may change prereproductive survival, energy may not be assimilated as quickly earlier in the year, the number of oocytes that can be matured at any one time may be limited to some extent by the space available in the body cavity, and so forth. But it can be claimed that theoretical predictions are consistent with what has been observed in certain natural situations.

VARIATION IN THE AGE AT MATURITY

I assumed above that all the individuals in a given population reproduce for the first time at the same age, but it is well known that in natural populations there is sometimes considerable variation in the age at maturity. This variation is potentially of great biological interest, because it concerns a character which always has some effect on fitness, and which under certain circumstances when the population is very rapidly increasing in numbers, for example—may be the single most important determinant of fitness (see Lewontin 1965).

In general, fitness is maximized by maturing as soon as possible. But in at least one set of circumstances often encountered in nature, this may not be so. Consider a species in which fecundity increases with age and in which immature animals survive better than adults. An animal which reproduces for the first time in a given year realizes a part of its total fitness at the cost of reducing the probability that it will survive to the following year. Further, by maturing for the first time in the following year, its fecundity when it did reproduce for the first time would be greater, since fecundity is assumed to increase with age. Clearly, it may be advantageous to delay maturity, depending on the ratio of juvenile to adult survival and on the rate at which fecundity increases with age. This idea can be expressed more precisely in mathematical terms.

Let us assume that any given animal matures at a years of age and that the earliest age at which maturity can possibly occur is a^* . We wish to calculate the rate of increase of animals maturing at a years of age. Inserting terms for survival, we can expand equation (1) to obtain

$$1 = e^{-ra}sc^{(a-a^*)}b(1 + pe^{-r} + \dots + p^w e^{-rw}).$$
(26)

Suppose that fecundity increases by some factor h per annum, so that $b(x + 1) = h \cdot b(x)$; of course $b(a) = h^{(a-a^*)}b(a^*)$, where $b(a^*)$ will be taken to be a constant. For convenience, we designate q = p/c. Equation (26) can then be rearranged to give

$$e^{ra} - hqc \cdot e^{r(a-1)} - sb(a^*)(ch)^{(a-a^*)} = 0.$$
⁽²⁷⁾

This is the general implicit equation for the rate of increase of individuals maturing at age a, under the conditions of the model. We now wish to know what the effect of a is on r when the other life history parameters are given, although it will, in fact, be found more convenient to use the finite rate of increase e' rather than r. Implicit differentiation of equation (27) yields

$$\frac{de^{\mathbf{r}}}{da} = \frac{sb(a^*)(ch)^{(a-a^*)} \cdot \ln (ch)}{e^{\mathbf{r}(a-1)}[a - hqc \cdot (a - 1)e^{-\mathbf{r}}]}.$$
(28)

Consider first the case in which juvenile and adult survival are equal (q = 1)and in which fecundity does not vary with age (h = 1). Since the annual rate of juvenile survival, c, is less than unity, $\ln ch < 0$. The derivative is therefore negative if $ae^{r(a-1)} > c(a - 1)e^{r(a-2)}$. This is invariably satisfied, provided that r is positive. In general, increasing the age at maturity will decrease the rate of increase of a population, as expected. But the derivative is positive in sign if $e^r < [c(a - 1)]/a$. Thus, a heritable tendency for delayed maturity may be favorably selected, even though fecundity is constant and juveniles survive at the same rate as adults, if the population is decreasing in numbers rather rapidly. This can be appreciated intuitively: for the same reason that animals with long generation times will increase in numbers relatively slowly, they will also decrease in numbers relatively slowly. If we allow h and q to differ from unity, the evolution of delayed maturity is possible even in an expanding population. For the derivative of equation (28) to be positive, numerator and denominator must be of like sign; thus r increases with a if $q > ae^{r}/[hc(a - 1)]$ and h < 1/c, or $q < ae^{r}/[hc(a - 1)]$ and h > 1/c.

Two caveats should be added to this conclusion. First, I assumed that a^* , the first possible age at maturity, is one; if this is not so, then *s* must refer to the survival between age zero and age a^* . Second, and more important, the model does not include any allowance for the energy cost of reproduction. If fecundity is proportional to size, and if the rate of growth in size is diminished by reproduction, an animal which matures at any given age will be less fecund in the following year than an animal reproducing for the first time in that year. This situation, which is probably common among poikilothermous vertebrates, will further favor the evolution of delayed maturity. It will be explored in a paper presently in preparation.

Thus, selection may favor an increase or a decrease in the age at maturity. It is clear from equation (28) that, because the derivative cannot be equated to zero, there is strictly no optimal age at maturity-not at least under the conditions of the model used. Instead, selection will tend to increase or decrease the age at maturity until selection is prevented from making further progress by factors inherent in the biology of the animal concerned. This process may lead to variation in the age at maturity both within and between populations and to secular changes in the mean age at maturity. All three phenomena have been observed in nature. Variation within populations is common in long-lived birds: examples are given by Hornberger (1957, white stork), Coulson and White (1958, kittiwake), Serventy (quoted in Lack 1966, p. 261, shearwater), Mertz (1971, condor), and many other authors. Variation among populations has been especially well documented in the salamander Desmognathus ochrophaeus (Tilley 1973) and in the trout (Alm 1949 and 1959). Changes in the age of maturity with time are more difficult to observe but seem to have occurred in heavily exploited whale populations (Gulland 1970). All these phenomena could be interpreted as adaptive responses to the selective forces that have been described above, and in many cases this interpretation is probably valid. Nevertheless, it is not a conclusion that should be drawn too lightly, since identical phenomena may be caused by nonselective agencies.

Suppose that all females in a population produce offspring among which the different phenotypes are represented in some constant ratio, a phenotype being maturation at a given age. That is, differences in the age at maturity exist but are not heritable. Let some of these offspring mature at a years of age and others at b, c, \ldots, z years of age. Individuals maturing at age a are called type A individuals, and so forth. For the case of a population in unrestricted exponen-

tial growth with no mortality at any stage, Cole (1960) obtained a difference equation in r:

$$1 = n_A e^{-ra} + n_B e^{-rb} + \dots + n_z e^{-r},$$
(29)

where n_A is the number of type A individuals per litter, and so forth. As this relationship holds not only for the population as a whole but also for any type within the population, the proportions of the different phenotypes will reach a stable distribution which is governed by the well-known equation discovered by Sharpe and Lotka (1911). Cole is then able to prove that, under the conditions of his population model, early-maturing phenotypes will be less common in the equilibrium population than late-maturing phenotypes. The situation can be treated more realistically by assuming the population to be stationary in size and to be undergoing real rates of mortality expressed by the terms for "larval," juvenile, and adult survival which have previously been defined. After a little algebra, we find that the fraction of animals age x which are of type A, $c_A(x)$ is given by

$$c_A(x) = f_A l(x) \left[\frac{(1-c)(1-p)}{(1-c)(1-p) + s(1-p) + sc^{(a-1)}p} \right],$$
 (30)

where f_A is the fraction of the offspring of any female which are of type A, and l(x) is of course a function of s, c, and p. The predictions of this equation are quite different from those of Cole's. It is governed largely by the value of s, the rate of survival during the first year of life; as s approaches zero, the stable frequencies of the different phenotypes approach the fixed offspring phenotype frequencies. Moreover, a change in s which acts equally on all phenotypes will change their stable frequencies in the population. Change in s will, therefore, be accompanied by secular change in phenotype frequencies; and differences in s among populations will cause differences in phenotype frequencies. Thus, nonselective changes in mortality acting on environmental variation in the age at maturity may mimic selection acting on heritable variation.

DISCUSSION

A very common criticism of mathematical arguments in biology is that by ignoring much of the complexity of matural populations they generate predictions which, while appearing to be general, rely on special sets of conditions rarely encountered in nature. This may be circumvented to some extent by, as Levins (1966) puts it, sacrificing generality of prediction for precision. For example, the general solution to Cole's result that was proposed in the first part of this paper is much more generally applicable to real populations than the original result; but as a result its consequences are more difficult to identify. One reason for this is that some of the parameters in equation (20) are explicitly dependent on time, which may be a common feature of fitness and fitness analogues (see Charlesworth 1970). The solution of equation (20) for a particular set of parameters is shown in figure 3; the simulation represents a population in which prereproductive survival is initially very high but declines monotonically to reach a constant value in the tenth cycle.¹ It can be seen that k fluctuates very considerably before settling down to a constant value as the population approaches age structure equilibrium when the value of prereproductive survival becomes constant. Even this is a gross underestimate of the complexity of any real situation, however, as the solution relies on the assumption that the life history parameters which determine the age distribution are themselves fixed or eventually become fixed. This is unlikely to be true in most real populations; and consequently the age structure, and with it k, will never reach constant values. The magnitude of this effect and its relevance to the evolution of the life history will depend on the biology of the particular organism being studied, but it is clear that any formal mathematical solution will be very difficult to discover when such a problem is stated in the most general terms.

One alternative to a formal solution is to specify a population of numbers, with properties thought to represent adequately those of a population of animals, and then to observe its behavior by numerical simulation on a computer. This has the advantage of getting somewhat closer to the natural situation and the disadvantage that shortcomings in the logic used to write the computer program are often more difficult to see than similar fallacies in

¹ The life table used for the iteroparous population was initially:

l(o) = 1		
l(1) = s = 0.9		
l(2) = 0.8s	b(2) = 10	l(2)b(2) = 7.2
l(3) = 0.4s	b(3) = 15	l(3)b(3) = 5.4
l(4) = 0.2s	b(4) = 25	l(4)b(4) = 4.5
l(5) = 0		
		x = w
		$\sum_{a} l(x)b(x) = 17.1$

This was taken to represent a newly founded colony growing very rapidly under near optimal conditions. The initial age structure essentially comprised newborn animals only, c(o) = 0.96. Small representation of later age classes was necessary for the program to be accepted. It was imagined that as exponential growth proceeded, the environment progressively deteriorated, causing a decrease in prereproductive survival, s. This occurred over a period of 10 cycles, at the end of which the population was stationary in numbers with:

$$\sum_{a}^{x=w} l(x)b(x) = 1.$$

This was done by generating a new value of s in every cycle:

$$s(j) = s(o) - \left\{\frac{s(o) - [s(o)/R_o]}{10}\right\} j,$$
$$R_o = \sum_{\Sigma}^{\infty = w} a(x)b(x).$$

where

When j = 10, $s(j) = s(o)(1/R_o)$, the value necessary to maintain a stationary population. In the semelparous population, it was required that fecundity and the age at maturity were the same as in the iteroparous population. The value of s(j) in semelparity was calculated from the equation given above, using $R_o = 17.1$, and not using the value of R_o in semelparity. In this way, the two populations remained comparable, and the calculation of k valid, throughout the simulation.

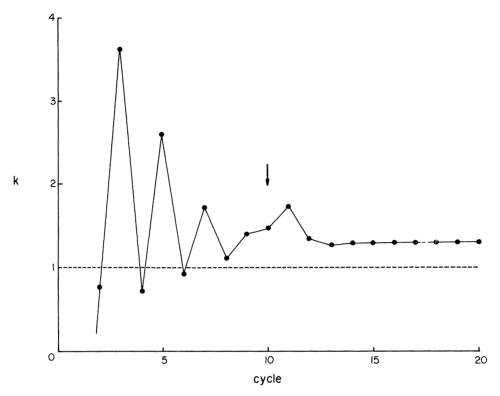


FIG. 3.—Exact solution of equation (20) for a given population model

formal mathematical analysis. This approach has been used by Murphy (1968) and by Hairston et al. (1970) to identify components of the fitness of iteroparity which cannot be deduced from simpler population models. Both assumed that the form of the life history was controlled by a single locus with two alleles, one homozygote conferring semelparity and the other iteroparity, the heterozygote being intermediate. All three genotypes were assigned the same net reproductive rate, and as a consebuence their absolute fitnesses in a given population were determined solely by their generation times. Murphy found that when in any given year the rate of prereproductive survival was put arbitrarily at 0.1 or 1, the more iteroparous phenotype was retained in the population when under a regime of some constant value of prereproductive survival it would have been lost. Hairston et al. criticized this experiment on the grounds that Murphy had introduced strong density-dependent mortality by setting an upper limit to population size and adjusting recruitment to this figure. Their simulation, which produced essentially the same result, included a constant birth rate and a rate of prereproductive survival which was a normally distributed random variable. Both experiments can be interpreted in the same way. It has been pointed out above that phenotypes with longer generation times will, in simple populations, increase in numbers less rapidly when the population as a whole is increasing rapidly and will decrease less rapidly when the population as a whole is decreasing. Thus, in the simulations of Murphy and of Hairston et al., the iteroparous phenotypes will have a smaller variance in r; this will cause a smaller variance in phenotype numbers (see Bartlett 1966), which is equivalent to a smaller probability of extinction. This kind of effect may well be important in environments which fluctuate with a cycle much shorter than the generation time of a given iteroparous life history.

Moreover, it can be shown that the genetic consequences of semelparity and iteroparity are somewhat different. Consider a population of annually breeding semelparous animals with some rate of prereproductive survival such that the population as a whole is stationary in size. Clearly, we have $e^r = (sb) \sim 1$. In each generation of sexual reproduction, the surviving progeny of a given parent are outcrossed to unrelated individuals-it is assumed for simplicity that no inbreeding occurs. The number of animals related by descent to an original parent (i.e., possessing any fraction of the original parental genome) is therefore doubled in each generation. If we write the rate of increase in the number of related individuals as u, then we have $e^{u} = 2(sb) \sim 2$. At the same time, the fraction of the original parental genome possessed by any descendant of the *n*th generation is exactly one-half of that possessed by a descendant of the (n-1)th generation. Thus, using w to mean the rate of increase of the original parental genome, we can write $e^w = [2(sb)]/2 = (sb) \sim 1$. That is, the original parental genome is conserved indefinitely when it is assumed that no selection takes place. In the iteroparous population with the same characteristic, except that adult animals survive with a frequency p per annum and breed in every year of their lives, we have, from equation (15), $e^r = (sb + p) \sim$ (1 + p). In each generation, each animal gives rise to (2sb + p) descendants its two surviving progeny plus its own probability of survival. Thus, $e^{u} =$ (2sb + p). The surviving progeny of any parent will be related to it by a factor of one-half, and of course if it survives it will be related to itself by a factor of one. Therefore $e^w = \{ [2(sb)/2] + p \} = (sb + p) \sim (1 + p)$. We can now compare semelparity and iteroparity with respect to increase in population size, in the number of descendants, and in the fraction of the parental genome transmitted:

$$\begin{aligned} e^{r_i}/e^{r_s} &= (sb + p)/(sb) \le 2\\ e^{u_i}/e^{u_s} &= (2sb + p)/(2sb) \le 1.5\\ e^{w_i}/e^{w_s} &= (sb + p)/(sb) \le 2. \end{aligned}$$

Then if we equate the rates of increase in number of the semelparous and iteroparous populations, we have $e^{u_i}/e^{u_s} = (2sb + p)/2(sb + p) < 1$. Thus, the number of descendants of an original parent will increase less rapidly in iteroparity than in semelparity; conversely, the mean relatedness of these descendants to the original parent is proportionately greater. Iteroparity, so to speak, involves putting more of one's genetic eggs into the same somatic basket.

Thus, the dynamics of selection on even an apparently simple life history

dichotomy may be very complex, and any attempt to test general mathematical theorems by reference to examples collated (sometimes, perhaps, rather selectively collated) from the literature may be seriously misleading. The identifiable predictions of theorems which are general enough to be interesting will rarely be sufficiently precise or sufficiently exclusive to be adequately tested in this way. This is not a counsel of despair, nor is it merely an appeal to the rather defensive mysticism sometimes professed by nonmathematical naturalists, nor is it a denial that broad biological generalizations occasionally achieve brilliant success. But it does suggest that the primary function of mathematics in biology lies, not in the statement of general laws, but rather in stimulating the imagination of the field naturalist. Only by reference to detailed observations of particular situations can the relevance of results such as those set out above be assessed. And if this is to be done, it cannot be urged too strongly that mathematical arguments should be presented so that they can be followed by an interested naturalist. No one should be obliged to ignore an argument or to take it on trust because its proponent is unable or unwilling to express it in terms that a layman can understand.

SUMMARY

L. C. Cole proved, for a particular population model, that a semelparous population with mean fecundity (b + 1) would have the same rate of increase as an indefinitely iteroparous population with mean fecundity (b). This result seemed so surprising that several attempts have since been made to reconcile it with reality. It is shown that they represent various special cases of a general equation which is derived from first principles and whose properties are explained. It is concluded that the evolution of iteroparity will be favored by a number of factors and particularly by delayed maturity and by reduction in the rate of survival during the first year of life.

Iteroparity is not a simple phenomenon; individuals may breed only once in a given year, they may breed several times, or they may breed almost continuously. The relative fitness of these strategies is defined, and it is suggested that almost continuous breeding is mot likely to evolve in animals which mature early in life and produce very large numbers of eggs.

In the third section, the consequences of variation in the age at maturity are explored. An equation is given which yields r for an individual maturing at any given age and is used to define conditions that r should increase with delayed maturity. These arguments emphasize the idea that, as the result of selection, the age at maturity may vary within and among populations and may also change with time. It is then shown that identical phenomena may be observed even if the age at maturity has no heritable component. It is concluded that variation in this character must be interpreted cautiously.

Finally, attention is drawn to the deficiencies of the simple population models used in this paper. The time dependence of certain terms in the general equations, the effects of variance in population size, and differences in the genetics of semelparity and iteroparity combine to make general predictions from simple models naive and precise predictions from general models difficult to identify. It is concluded that ideas such as those presented here can be tested adequately only by detailed reference to particular situations.

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