OPTIMAL REPRODUCTIVE EFFORT IN FLUCTUATING ENVIRONMENTS

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Although discussion of the evolutionary consequences of environmental fluctuations has recently become popular (e.g., Levins 1967; Fretwell 1972), many theoretical treatments of optimal life histories (e.g., Emlen 1970; Gadgil and Bossert 1970; Schaffer 1974) remain restricted by assumptions of environmental constancy. Here I relax these restrictions for the special case in which fecundity and mortality rates do not vary with age. Briefly, I show that if, in constant environments, repeated breeding (iteroparity) is the optimal reproductive strategy, environmentally induced variation in reproductive success favors reductions in per capita reproductive output. Conversely, variations in postbreeding survival among adults favor greater investments in breeding. Cohen (1966, 1968) reached similar conclusions regarding the optimal *fraction* of individuals in a population that should germinate or reproduce in a given year. Relating Cohen's work to mine, I show that such a mixed strategy is generally optimal only if in a constant environment the optimal reproductive expenditure is 100%, that is, only if individuals die after a single breeding (semelparity). Both Cohen's results and those presented here suggest that generalizations common in the literature—namely, that fluctuating environments *always* favor greater reproduction, whereas constant environments *always* select for small litters and increased longevity (e.g., Pianka 1972)—are not deducible from theory. Rather, they suggest that the age-specificity of the fluctuations (do they principally affect immatures or adults?) is the principal issue. This result marches well with conclusions of Schaffer (1974) regarding the selective impact of environmentally induced changes in life tables in constant environments and with Menge's (1974) empirical studies of the reproductive response of sea stars to wave action. Murphy (1968) made similar assertions. Unfortunately, these were based in part on computer simulations that were later challenged by Hairston et al. (1970). In fact, Murphy's conclusions are entirely correct in this regard, and the criticism raised against them is without substantial merit.

ANALYSIS

In a species without age structure, an individual's fitness equals the annual contribution it makes to the population. This contribution, which

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I denote by λ, is the number of offspring produced that survive to breed the following year added to the probability that the individual in question itself survives to the next breeding season. Thus,

$$\lambda = B + P \tag{1}$$

(Schaffer 1974), where B is the effective litter size and P the rate at which adults survive from one breeding season to the next. (In a phenotypically homogeneous population, $N[t+1] = \lambda N[t]$.)

In a constant environment, an optimal reproductive strategy maximizes the sum $B + P$. These parameters may usefully be assumed to depend on reproductive effort (Williams 1966; Gadgil and Bossert 1970; Calow 1973). If the functions $B(E)$ and $P(E)$ are concave, that is, have negative second derivatives (fig. 1a), the optimal effort value, $\hat{E}$ is likely to be intermediate between 0 and 100% (iteroparity). In this case, $\hat{E}$ satisfies the relation

$$\frac{dB}{dE} = -\frac{dP}{dE} \tag{2}$$

(fig. 1b). On the other hand, if $B(E)$ and $P(E)$ are convex (fig. 1c), the optimal effort will be 100% (semelparity), save in those cases where $B(100\%) < P(0)$. (Since $P[0] \leqslant 1$, such populations always go extinct and need not be considered.)

In a fluctuating environment, $B(E)$ and $P(E)$ vary from year to year. In this case, the long-term rate, $\bar{\lambda}$, at which a population multiplies is given by the expression

$$\ln \bar{\lambda} = \sum_0^\infty q_i \ln \lambda_i \tag{3}$$

(Levins 1967). Here, q's refer to frequencies of different values of λ. Equation (3) follows from the observation that at time T, the population's size is

$$N(T) = (\lambda_1^{t_1}\lambda_2^{t_2}\lambda_3^{t_3} \ldots \lambda_n^{t_n})N(0)$$
$$= \bar{\lambda}^T N(0),$$

where t_i is the number of years that the population multiplies at rate λ_i and $\Sigma t_i = T$. As a result,

$$\bar{\lambda} = \lambda_1^{q_1} \lambda_2^{q_2} \ldots \lambda_n^{q_n}$$

from which equation (3) follows directly. Accordingly, it is of interest to calculate the effort value, $\hat{E}_F$, that maximizes $\bar{\lambda}$. In the simplest case (which nonetheless exhibits the properties I wish to consider) there are only two environmental states, good years and bad, randomly distributed and with equal frequency. Then,

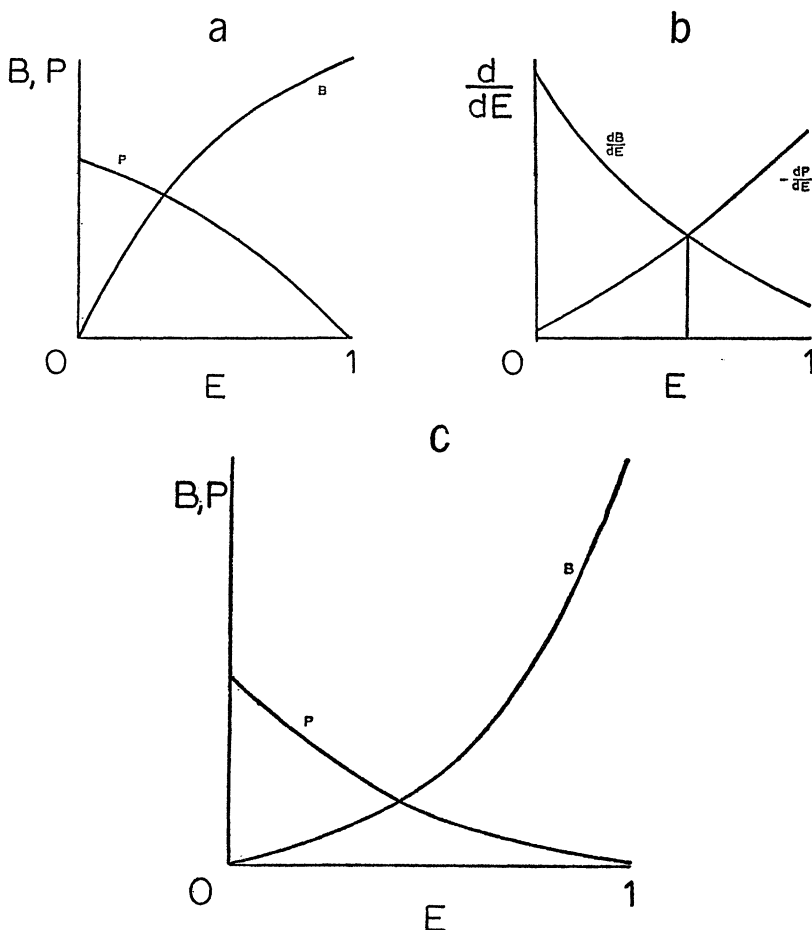$$\bar{\lambda}^2 = (\lambda_g)(\lambda_b). \tag{4}$$

FIG. 1.—Optimal reproductive effort in constant environments. *a*, Effective litter size, *B*, and postbreeding survival, *P* plotted against reproductive effort, *E*. Curves are concave, and the effort value, $\hat{E}$, maximizing $B + P$ ($=$ yearly rate at which population multiplies), intermediate between 0 and 100%—selects for iteroparity. *b*, For *concave B* and *P*, $\hat{E}$ satisfies the relation $(dB/dE) = -(dP/dE)$. *c*, *B* and *P* plotted against reproductive effort, but curves are convex. $\hat{E} = 100\%$—selects for semelparity.

If reproductive success is the only parameter affected by the environmental variation, we may write

$$\lambda_g = B(1 + s) + P, \qquad (5a)$$

$$\lambda_b = B(1 - s) + P, \qquad (5b)$$

where *s* measures the departure of good and bad years from the arithmetic mean, which is held constant. To determine the manner in which $\hat{E}_F$ varies with *s*, note that

$$\bar{\lambda}^2 = (B + P)^2 - s^2 B^2; \qquad (6)$$

and if $B(E)$ and $P(E)$ are concave (iteroparity), $\hat{E}_F$ satisfies the relation

$$\left(1 - \frac{s^2 B}{B+P}\right)\frac{dB}{dE} = -\frac{dP}{dE}. \tag{7}$$

Thus, $\hat{E}_F$ varies inversely with s (fig. 2a). Conversely, if adult survival is the sole parameter affected by environmental change, we have

$$\lambda_g = B + P(1+s), \tag{8a}$$

$$\lambda_b = B + P(1-s), \tag{8b}$$

and

$$\bar{\lambda}^2 = (B+P)^2 - s^2 P^2. \tag{9}$$

In this case, $\hat{E}_F$ satisfies the relation

$$\frac{dB}{dE} = -\left(1 - \frac{s^2 P}{B+P}\right)\frac{dP}{dE}, \tag{10}$$

with the consequence that increasing environmental variance favors greater reproductive output (fig. 2b).

Mixed versus Monomorphic Populations

As indicated earlier, the preceding results closely parallel those of Cohen (1966, 1968), who computed the optimal fraction of a population that should germinate or reproduce annually. Under what circumstances does such a mixed strategy confer greater fitness than the monomorphic response described above? We can answer this question quite readily using the method of fitness sets devised by Levins (1967). To do this, plot $\lambda_g(E)$ against $\lambda_b(E)$ for all E values (fig. 3). The resulting figure gives the rates of increase in both environments of all E phenotypes, and thus also the
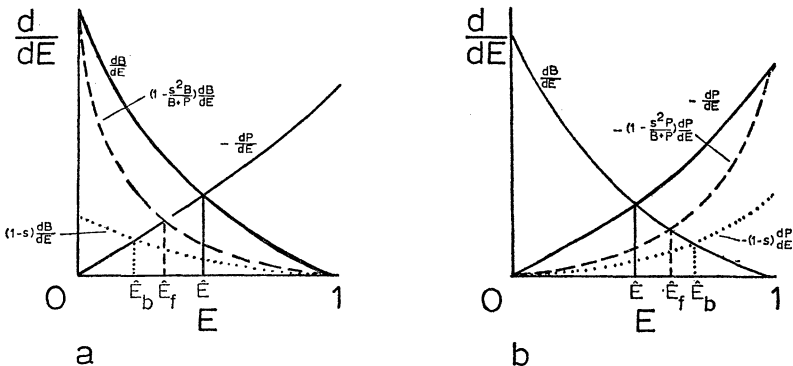

Fig. 2.—Optimal effort, $\hat{E}_F$, for an iteroparous organism in a fluctuating environment. a, Reproductive effort variable. $\hat{E}_F < \hat{E}$. b, Postbreeding survival variable $\hat{E}_F > \hat{E}$. In both graphs, dotted lines indicate optimal effort in bad years, $\hat{E}_b$.
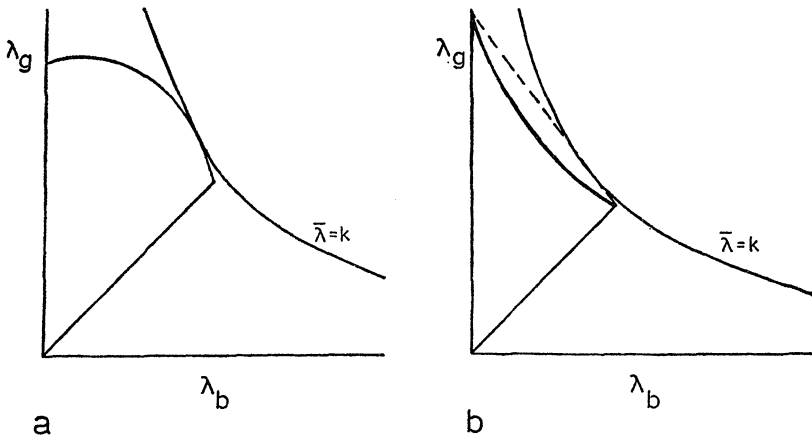
FIG. 3.—The fitness set λ_g (E) vs. λ_b (E) plotted for all E values. $s = 1$. Reproductive success variable, a, $B(E)$ and $P(E)$ are concave (iteroparity in constant environments) and the fitness set is convex. Optimal population monomorphic (see fig. 2a), being the point on the fitness set tangent to $\bar{\lambda} = k$ of largest k. b. $B(E)$ and $P(E)$ are convex (semelparity in constant environments), and the fitness set is concave. Optimal population can be polymorphic. Each year only a fraction of potential breeders reproduce, and these make a 100% effort, i.e., organisms breed at different ages (see text for further details).

strategy that maximizes $\bar{\lambda}$. For if the fitness set is convex (fig. 3a), the optimal population is monomorphic, being the point on the margin tangent to the adaptive function, $(\lambda_g)^{1/2} (\lambda_b)^{1/2} = k$ of largest k. On the other hand, if the fitness set is concave (fig. 3b), the optimal population can be polymorphic, consisting each year of some individuals which reproduce at the maximal rate, $E = 100\%$, and others which do not breed at all.[1] By using the relation

$$\frac{d^2\lambda_g}{d\lambda_b^2} = \frac{(d\lambda_b/dE)(d^2\lambda_g/dE^2) - (d\lambda_g/dE)(d^2\lambda_b/dE^2)}{(d\lambda_b/dE)^3}, \qquad (11)$$

which, if fecundity is the parameter affected by the fluctuations, reduces to

$$\frac{d^2\lambda_g}{d\lambda_b^2} = -\frac{2s[(dB/dE)(d^2P/dE^2) - (dP/dE)(d^2B/dE^2)]}{[(1-s)\,dB/dE + dP/dE]^3}, \qquad (12)$$

[1] The basis for this assertion is discussed by Levins (1967). Briefly, Levins argues that a line connecting two points on the margin of the fitness set represents a series of mixtures of the two marginal phenotypes. When the fitness is concave, a point on this line can be tangent to an adaptive function, $(\lambda_g)^{1/2} (\lambda_b)^{1/2} = k$ of greater k than any point on the margin itself. Note that Levins' technique merely characterizes the optimal population. It does not provide a mechanism for maintaining the mixture. For example, if the horns of the fitness set represent alternative alleles, one will soon be lost because of a run of good or bad years. To preserve the polymorphism from such vagaries, a more complex genetic system must be involved, one in which the same genotype produces both morphs.

one can readily show that if the second derivatives (d^2B/dE^2) and (d^2P/dE^2) are everywhere negative (iteroparity in constant environments), the fitness set will be convex and the optimal population in a fluctuating environment monomorphic (fig. 3a), being defined by equation (7). On the other hand, if the second derivatives (d^2B/dE^2) and (d^2P/dE^2) are everywhere positive (semelparity in constant environments), the fitness set will be concave. In this case, the optimal fraction, $\hat{r}$, of individuals breeding yearly is

$$\hat{r} = 0, \qquad\qquad\qquad P/B \geqslant 1$$

$$\hat{r} = \frac{P}{B}\left(\frac{1 - P/B}{s^2 - (1 - P/B)^2}\right), \quad 1 > P/B > (1 - s^2) \qquad (13)$$

$$\hat{r} = 1, \qquad\qquad\qquad P/B \leqslant (1 - s^2)$$

where $P = P(0)$ and $B = B(100\%)$. Equations (13) follow from setting

$$\frac{\partial \bar{\lambda}(r,s)}{\partial r} = 0,$$

where

$$\begin{aligned}\bar{\lambda}^2 (r,s) &= [r(1 + s) B + (1 - r) P][r(1 - s) B + (1 - r) P]\\ &= [rB + (1 - r) P]^2 - (rsB)^2.\end{aligned} \qquad (14)$$

Thus, increasing s, as well as the ratio P/B, will select for reducing the fraction of individuals breeding yearly.

DISCUSSION

These results support Murphy's (1968) contention that environmentally induced variations in reproductive success favor reduced breeding in iteroparous species and thus greater longevity and a longer reproductive lifespan. Additionally, they suggest that the objections raised by Hairston et al. (1970) to Murphy's computational techniques do not invalidate his major conclusion. On the other hand, as Pianka (1972) has observed, Hairston and his associates are correct in stressing the importance of determining whether reproductive success or adult survival is the parameter principally affected by the fluctuations. In sum, there seems to be no justification for assuming that increased environmental uncertainty *necessarily* selects for increased reproductive output. No doubt, this may often be the case, since such fluctuations reduce crowding, which, in turn, may principally affect the chances of successful breeding or, equivalently, survival among immatures (Gadgil and Solbrig 1972; Schaffer and Gadgil 1975). On the other hand, exceptions to the "general rule" are also to be expected. Thus, Menge (1974) has recently documented a case in which increased density-independent mortality—wave action acting on sea stars—has apparently selected for reduced reproductive effort, because brooding females are apt to lose their entire clutch in turbulent waters. To reiterate, it is the age-

specificity of the mortality, constant or fluctuating, that determines the adaptive response.

Before closing this discussion, I return briefly to the concept of fitness which I rather cavalierly equated with the geometric mean rate of increase. Although this is a common device, it is worthwhile to observe that other authors have suggested the appropriateness of different criteria. In particular, Lewontin (1965) and Slobodkin (1964) have suggested that the best measure of a genotype's or population's long-term fitness is its expected longevity, or the probability that it will not go extinct during the course of a certain period of time. Roughly, the result of applying this criterion to the present problem is to place greater emphasis on the rate of increase in bad years (fig. 2, dotted lines). As a consequence, the predictions made on the basis of maximizing $\bar{\lambda}$ will be qualitatively unchanged but quantitatively more dramatic. Uncertainty in reproduction will select for an even greater reduction in per capita reproduction or in the proportion of individuals breeding yearly, etc. Presently, this aspect of the problem is being pursued by R. Griego and D. Mason, who were kind enough to explore the matter with me.

SUMMARY

When the life history functions $B(E)$ and $P(E)$—fecundity and post-breeding survival—are subject to environmentally induced fluctuations, one of two patterns is selected for: If the functions are concave (iteroparity in constant environments), the optimal population is monomorphic. Variation in $B(E)$ selects for reduced effort in all individuals; variation in $P(E)$ for increased breeding. If functions are convex (semelparity in constant environments) and fecundity is the parameter at issue, the optimal population can be polymorphic, with only a fraction of the population reproducing annually. Increasing the severity of fluctuations reduces the optimal value of this proportion, even if the average rate of reproductive success is not changed.

ACKNOWLEDGMENTS

LITERATURE CITED

Calow, P. 1973. The relationship between fecundity, phenology, and longevity: a systems approach. Amer. Natur. 107:559–574.
Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. J. Theoret. Biol. 12:119–129.

————. 1968. A general model of optimal reproduction in a randomly varying environment. J. Ecol. 56:219–228.

Emlen, J. M. 1970. Age specificity and ecological theory. Ecology 51:588–601.

Fretwell, S. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, N.J. 217 pp.

Gadgil, M., and W. H. Bossert. 1970. Life historical consequences of natural selection. Amer. Natur. 104:1–24.

Gadgil, M., and O. T. Solbrig. 1972. The concept of r- and K-selection: evidence from wildflowers and some theoretical considerations. Amer. Natur. 106:14–31.

Hairston, N. G., D. W. Tinkle, and H. M. Wilbur. 1970. Natural selection and the parameters of population growth. J. Wildlife Manage. 34:681–690.

Levins, R. 1967. Evolution in changing environments. Princeton University Press, Princeton, N.J. 120 pp.

Lewontin, R. C. 1965. Selection in and of populations. Pages 299–311 in J. A. Moore, ed. Ideas in modern biology. Natural History Press, New York.

Menge, B. A. 1974. Effect of wave action and competition on brooding and reproductive effort in the sea star *Leptasterias hexactis*. Ecology 55:84–93.

Murphy, G. I. 1968. Pattern in life history and the environment. Amer. Natur. 102:390–404.

Pianka, E. R. 1972. r and K selection or b and d selection? Amer. Natur. 106:581–588.

Schaffer, W. M. 1974. Selection for optimal life histories, the effects of age structure. Ecology 55:291–303.

Schaffer, W. M., and M. D. Gadgil. 1975. Selection for optimal life histories in plants. In M. Cody and J. Diamond, eds. The ecology and evolution of communities. Harvard University Press, Cambridge, Mass. (in press).

Slobodkin, L. B. 1964. The strategy of evolution. Amer. Sci. 52:342–357.

Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, N.J. 307 pp.