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LIFE-HISTORY TACTICS: A REVIEW OF THE IDEAS

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ABSTRACT

This review organizes ideas on the evolution of life histories. The key life-history traits are brood size, size of young, the age distribution of reproductive effort, the interaction of reproductive effort with adult mortality, and the variation in these traits among an individual's progeny. The general theoretical problem is to predict which combinations of traits will evolve in organisms living in specified circumstances.

First consider single traits. Theorists have made the following predictions: (1) Where adult exceeds juvenile mortality, the organism should reproduce only once in its lifetime. Where juvenile exceeds adult mortality, the organism should reproduce several times. (2) Brood size should maximize the number of young surviving to maturity, summed over the lifetime of the parent. But when optimum brood-size varies unpredictably in time, smaller broods should be favored because they decrease the chances of total failure on a given attempt. (3) In expanding populations, selection should minimize age at maturity. In stable populations, when reproductive success depends on size, age, or social status, or when adult exceeds juvenile mortality, then maturation should be delayed, as it should be in declining populations. (4) Young should increase in size at birth with increased predation risk, and decrease in size with increased resource availability.

Theorists have also predicted that only particular combinations of traits should occur in specified circumstances. (5) In growing populations, age at maturity should be minimized, reproductive effort concentrated early in life, and brood size increased. (6) One view holds that in stable environments, late maturity, multiple broods, a few, large young, parental care, and small reproductive efforts should be favored (K-selection). In fluctuating environments, early maturity, many small young, reduced parental care, and large reproductive efforts should be favored (r-selection). (7) But another view holds that when juvenile mortality fluctuates more than adult mortality, the traits associated with stable and fluctuating environments should be reversed.

We need experiments that test the assumptions and predictions reviewed here, more comprehensive theory that makes more readily falsifiable predictions, and examination of different definitions of fitness.

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GLOSSARY

Bet-hedging: An alternative *explanation* for the trends explained by *r*-selection and *K*-selection, based on the analysis of fluctuations in adult and juvenile mortalities.

b_x : Average number of young born to a female aged x .

Cost of reproduction: The marginal increase in adult mortality between time t and time $t + 1$ caused by the decision to commit a certain proportion of available resources to reproduction at time t .

Fitness: Something everyone understands but no one can define precisely.

Iteroparity: Repeat reproduction, giving birth several times in a lifetime. The perennial habit.

K: Equilibrium density, the number of individuals present under constant conditions when population fluctuations have died down. May be lower than saturation density, the number of individuals that the environment could conceivably maintain.

K-selection: Either a *label* applied to the combination of late maturity, few, large young, a long life, and small reproductive efforts (as in "*K*-selected"), or an implied *explanation* of why those traits are found together. Which meaning is being used is rarely specified.

l_x : Probability of surviving to age x .

r : The intrinsic rate of natural increase under a stable age distribution, as defined by Lotka's equation,

$$1 = \int_0^{\infty} e^{-rx} l_x b_x dx.$$

r-selection: Either a *label* applied to the combination of early maturity, many, small young, a short life, and large reproductive efforts (as in "*r*-selected"), or an implied *explanation* of why those traits are found together. Which meaning is being used is rarely specified.

Reproductive effort: The proportion of resources diverted to reproduction, summed over the time interval in question.

Reproductive value: The present value of future offspring implied by the current population growth rate, or, the average number of young a female (aged x) can expect to have over the rest of her life, discounted back to the present. Usually denoted V_x or v_x/v_0 .

Semelparity: The big-bang reproductive pattern; giving birth only once and committing suicide in the process. When done in the first year of life, the annual habit.

Stable age distribution: The unique distribution of organisms among age classes that a population will reach on a fixed schedule relating fecundity and mortality to age.

Tactic: A set of coadapted traits designed, by natural selection, to solve particular ecological problems. A complex adaptation.

INTRODUCTION

Scope and Purpose

AT THE center of the evolutionary paradigm lies the definition of fitness. Fit organisms are defined as those better represented in future generations than their relatively unfit competitors. Evolution places heavy emphasis on reproduction, for the way an organism reproduces affects profoundly its contribution to future generations. Reproduction is not the only component of fitness, but it is certainly an important one.

Between 1954 and 1973, intense theoretical activity produced a welter of hypotheses relating observed trends in reproduction to various causes. The ideas put forth a posteriori as explanations of field observations rapidly outstripped their empirical base and grew into a

tangled thicket that blocked further progress. To date, few workers have shown any inclination to start the pruning and cutting process of experimentation that will shape this tangled thicket of ideas into clear explanations.

Throughout this essay, I shall refer to this area of biology as the theory of life-history tactics, or life-history tactics, for short. The phenomena studied naturally elicit a research viewpoint that combines the study of reproduction, growth, and genetics in an ecological setting to produce hypotheses concerning evolutionary changes. I define a tactic as a set of coadapted traits designed, by natural selection, to solve particular ecological problems. For example, the life-history tactic of a population of fish living in a lake might consist of its age-specific distribution of growth rates, reproductive efforts, progeny produced and their

size, and the genetic system underlying those traits.

Another review of life-history tactics is waiting to be written. It would take the hypotheses reviewed in this paper, or their surviving descendants, and test them against the massive body of evidence accumulated on *Drosophila*, *Tribolium*, cultivated plants, domestic livestock, and exploited fish populations. I have not attempted to summarize that body of data in this paper, which has grown bulky without it, but I hope someone will.

Thus this paper has a restricted goal: to review most of the current ideas about life-history tactics, and some of the data bearing on them. I seek not to evaluate the ideas against the evidence, but to bring order to a field whose natural complexity has been compounded by a proliferation of viewpoints. I have tried to write the paper that I wanted to read, but could not find, when I started my own study of life histories. I have addressed myself primarily to those seeking an introduction to the field. The review includes papers that come to my attention prior to May, 1974.

The Problem

How can we predict what measurable traits populations will evolve in any particular real situation? Three things strike me as important. First, the answer depends to a large extent on the quality of information we can get. Thus we should develop hypotheses with our capacities for measurement in mind. Second, we must agree on what we mean by "evolutionary situation" and "measurable traits." In the language of systems analysis, we must define concretely the state variables and the system parameters. In this review, I will consider some reproductive state variables (biological traits) and some system parameters (environmental conditions). Others have yet to be defined. Third, in order to discuss these issues, we must agree on the general nature of the problems facing evolving organisms. Williams (1966a) put it well: "The central biological problem is not survival as such, but design for survival."

In dealing with these problems, it is important to keep certain distinctions in mind. Some traits are so basic to the biology of a species that they do not vary within populations. All sparrows have wings, and all men have two legs.

Such traits take a long time to evolve. Other traits vary, and can be fine-tuned by selection to adapt individuals belonging to different populations of a single species to varying circumstances. Such traits can evolve rapidly. For the basic traits, the best type of explanation we can generate argues from broad comparisons among groups of taxa that have encountered different conditions over long periods of evolutionary time. This is the comparative approach to an explanation of adaptation. But the variable traits are open to explanations that proceed through deductive models to the test of risky, potentially falsifiable hypotheses in selection experiments. The immediate evidence from intraspecific selection experiments is much stronger than correlative evidence from interspecific comparisons. For we can tightly control the situations encountered by the animals, and since the animals all belong to a single species, the rest of the biology of the animals is controlled.

Conclusions reached from experimental tests of risky hypotheses can advance our knowledge by pointing out weaknesses in our models. It is much more difficult to falsify a prediction made at the interspecific level, where one can always argue that confounding effects obscure the main trend. But generalizations made from experiments carried out on a single species are subject to question, perhaps more so than generalizations based on correlations drawn from many species. The more certain we are that we know what is causing an evolutionary trend, the less certain we are that the cause is general. And the more certain we are that a trend is in fact general, the less certain we can be about its cause or causes. In living within these limits, I feel strongly that we must do experiments wherever possible, and base our arguments on the best evidence available whenever experiments are not possible, rather than resort to appealing to the beauty of untested speculations.

This paper reviews both comparative and experimental explanations of life-history tactics. Our knowledge will advance most rapidly through the interaction of theory and experiment at the intraspecific level. Many traits may appear to be fundamental, incapable of rapid evolution, and subject only to the comparative approach. But we should adopt the attitude that any variable trait can evolve rapidly and

is subject to experimentation, in order to minimize the number of manipulable traits that go unmanipulated. Nevertheless, our appreciation of a species's biology would be incomplete and unsatisfying without complementary explanations pitched at the interspecific level.

In order to arrive at testable predictions, we commonly assume that selection will push a population towards a combination of traits which represents an optimal tactic for that situation. However, nothing guarantees that the population will attain the optimal tactic. For as the environment changes, the population evolves, and as the population evolves the individual organism's perception and definition of the environment changes. We can assume that selection elicits local optima from the variability available in the population, but we have no guarantee that the local optimum attained will match predictions made from models that do not account for the limits of natural variability.

We can only measure life-history tactics on populations, not on individuals, for the variance among individual patterns is one of the most important elements of a tactic, and is only measurable on populations. Nevertheless, such variance is the product of selection acting on individual organisms, not on populations of them. By defining tactic as I have, I certainly have not meant to circumvent the importance of individual selection, which remains the basis of the phenomena to be explained.

With respect to reproduction, several biological decisions are important. How many times should I try to reproduce during my life? How many young should I have per brood? How old should I be when I first reproduce? Should I have a few large or many small young? How much variability in each of these traits should there be among my progeny? In essence, the theory of life-history tactics tries to predict the best decisions to make in the face of problems posed by different situations. After giving a short historical development of the subject, I will consider the first three questions in turn, then deal with the last two, and others, in a more complex context.

Throughout this paper I use r to indicate intrinsic rate of natural increase under a stable age distribution, R_0 to indicate the multiplicative rate per generation, and K to represent the carrying capacity of the environment in

numbers of individuals, as defined in the Lotka-Volterra equations. We can define r by a mathematical relationship among physiological parameters' (see below, p. 7 ff.), but it is probably best measured for populations in the field as the rate of increase in numbers at low population density. The two definitions have no necessary logical relationship. It is likely that every field measurement will yield a different value of r , while in theoretical work r is usually regarded as a fixed parameter characteristic of a species, population, or genotype. Similar comments apply to K .

In life-history theory, r is used as a phenotypic parameter (as it is in human genetics), not as a population parameter. The usual model implicitly deals with a population as though it were a set of asexually reproducing clones (C_1, C_2, \dots, C_n), each possessing a different r (r_1, r_2, \dots, r_n), and asks which clone will win out in competition under given conditions. This comment applies to traits other than r , and I emphasize that most models dealt with in this paper make this implicit assumption. It is done for reasons of mathematical tractability, for the alternative of dealing with sexual recombination explicitly is overwhelmingly complex. But the assumption seriously limits the models that use it. As a weak link in the chain of evolutionary logic, our failure to deal realistically with sex deserves wider discussion.

This paper requires some understanding of demography and population models. Among recent treatments for biologists, those in Krebs (1972) and Mertz (1970) are particularly lucid. Laughlin (1965), Caughley (1966), and Caughley and Birch (1971) have given useful critiques of the various definitions of population growth-rates and their relative merits in different contexts.

A BRIEF HISTORY

The theory of life-history tactics splits logically into three parts: (1) defining important biological traits; (2) representing these traits in mathematical form and developing mathematical tools for their formal manipulation; and (3) deducing predictions from the mathematical relations defined by the theory. These three areas have developed neither in parallel nor in series, but in a complex web.

The Stable Age Distribution

In 1907, Lotka established that there is a certain age distribution to which a population will tend, given a fixed life table, a fixed sex ratio, and a fixed schedule of age-specific fecundity. (Euler anticipated this result in 1760.) In 1911, Sharpe and Lotka proved that this age distribution is stable, and in 1925, in *The Elements Of Physical Biology*, Lotka summarized contemporary demographic knowledge. In that book he suggested that the birth-rate is not only an adaptive trait capable of being modified by natural selection, but is adjusted to an intermediate optimum (see Chapter X, p. 128, Dover edition).

The Intrinsic Rate of Increase, r

How is the growth rate of a population related to its age structure, and to the different probabilities of giving birth and of dying at different ages? Define l_x as the probability of surviving to age x , and b_x as the instantaneous birth-rate ($b_x dx$ is the number of female offspring born to females of age x to $x + dx$). Assume a stable age distribution. Now consider the number, $n_0(t)$, of newborn individuals at time t . In order to be newborn at time t , an individual must have had parents who were newborn at time $t - k$, and these parents must have survived to age k and have given birth. Thus,

$$n_0(t) = \int_0^{\infty} n_0(t - k) l_k b_k dk.$$

If we assume that the number of newborn progeny grows exponentially in time,

$$n_0(t) = ke^{rt}, \text{ then}$$

$$ke^{rt} = \int_0^{\infty} ke^{r(t-k)} l_k b_k dk, \text{ and}$$

$$1 = \int_0^{\infty} e^{-rk} l_k b_k dk.$$

This equation, known as Lotka's equation or the characteristic equation, was first derived by Lotka in 1913 (Lotka, 1913), The characteristic equation, which relates the life table and fecundity schedule of a population in stable age distribution to its growth rate, r , has been central to most subsequent theoretical work.

The Comparative Study of Life Tables

Raymond Pearl's influential books (1922, 1925, 1928, 1939) emphasized the comparative approach. He showed that maximum duration of life and the age-specific schedule of births and deaths vary both within and between species. In several species, including man and *Drosophila*, life-history traits show fairly high heritability. In 1935, Pearl and Miner reviewed the life tables of four invertebrates, as measured in the laboratory. They proposed that there are, in general, five possible types of mortality curves, of which three are common in nature: those where the major portion of mortality falls late in life, early in life (j -shaped), or constantly throughout life (diagonal).

Although Lotka and Pearl had urged a comparative approach, most life-history studies prior to 1940 concentrated on human populations. Deevey (1947) introduced ecologists to comparative demography. He reviewed the construction of life tables by three different methods, and pointed out that the few life tables available on different species could be broken into Pearl's three patterns of survivorship. He raised the hope, now partially realized, of discerning general ecological relationships through a study of life tables. Following Deevey's paper, the construction of life tables, either as an end in itself or to estimate r , became popular. Caughley (1966) and Caughley and Birch (1971) have recently offered valuable criticisms of the techniques used in constructing life tables and the problems encountered in interpreting them.

Reproductive Value

Fisher (1930) defined and emphasized the importance of the relative reproductive value of different age classes. He developed the idea by analogy with the concept of present value of money invested at compound interest. The reproductive value, $V_x = v_x/v_0$, of a female of age x , relative to that of a female at birth, consists of the average number of young a female of that age can expect to have over the remainder of her life, discounted back to the present. The formula is worth reproducing. MacArthur and Wilson (1967, pp. 89-91) give a derivation:

$$v_x/v_0 = (e^{rx}/l_x) \int_0^\infty e^{-rt} l_t b_t dt.$$

Females at maximal reproductive value should contribute most, per capita, to population growth, and, therefore, should be most sensitive to natural selection in a growing population (Cody, 1971). They should, for example, be at optimal age for dispersal (MacArthur and Wilson, 1967). The idea of reproductive value is significant because it allows us to characterize different age classes as being "worth" more or less in terms of their contribution to the intrinsic growth rate of the population, r . However, the reproductive value of a female is the present value of her future daughters only when both the female and her daughters are members of a population in stable age distribution (Leslie, 1948).

Leslie defined the reproductive value for a whole population, V , as the sum of the reproductive values of all age classes. In the discrete form,

$$V = \sum_{x=0}^{\infty} v_x/v_0 = \sum_{x=0}^{\infty} \left[\frac{e^{rx}}{l_x} \sum_{k=x+1}^{\infty} e^{-rk} l_k b_k dk \right].$$

Thus V , like r , permits comparison of the value of different age structures to growing populations. For continuous breeders, Fisher (1930) proved that

$$\frac{dV_t}{dt} = rV_t.$$

This remarkable equation holds for any age distribution, stable or not, and implies that the reproductive value of a population always increases at the rate (r) at which population numbers will grow when the stable age distribution implied by the current life table is reached (Mertz, 1970). For the discrete case, Leslie (1948, pp. 220–221) devised the analogous proof. Let A be the population projection matrix and $V(t)$ be a row vector of reproductive values for each age class. Then

$$V(t)A = V(t+1),$$

and

$$V(t+1) = \lambda V(t)$$

where λ is the dominant eigenvalue of the matrix A ($\lambda = e^r$). The idea is beautiful, but in nature spatial and temporal variability in the environment make it unlikely that one would

ever be able to measure a single representative r .

Vandermeer (1968) and Caughley (1970) have both commented on the meaning of reproductive value. Caughley has pointed out that it can be interpreted either as "(a) the number of females alive at some future time that will be descended from a female currently aged x , relative to the number of surviving descendants of her newborn contemporary," (p. 214) or as "(b) the number of females born, at the moment of measurement, to females aged x or older, per female aged x " (p. 214). Interpretation (b) is Vandermeer's version of a "reproductive value" with an intuitive meaning that is easily calculable and not too far wrong, so long as the age distribution is close to stable. As both Leslie (1948) and Caughley (1970) noted, interpretation (a) is true only for populations in stable age distribution.

Narrowing the Viewpoint: Leslie and Cole

Between 1910 and 1940, the idea emerged that a life history is a set of adaptive traits connected by relations that can be mathematically analyzed. Concurrently, demographers and statisticians were developing mathematical tools that permit extensive and sophisticated manipulation of model life histories. Two authors catalyzed the theoretical work. Leslie (1945, 1948) showed that, given the current population age structure and a known schedule of survival and number of births per thousand females of reproductive age, one could predict the detailed future growth of the population by means of matrix methods. [Lewis (1942) got the same result, but published in a relatively inaccessible journal.] This step introduced linear transformations to demography, and opened the subject up to the analytic techniques of stochastic process theory. Renewal theory constitutes the other main line of mathematical thought that is applicable to life histories. Keyfitz (1968) outlined the formal development of matrix methods and renewal theory and compared their usefulness in different settings, while Bartlett (1970) has presented a useful review of stochastic models in demography.

Cole (1954) emphasized the importance of age at first reproduction in determining population growth rate, r . In examining the sensitivity of r to changes in birth-rate and age at first reproduction, he unveiled an apparent para-

dox. Giving birth to $n + 1$ offspring, and then dying, is equivalent, in so far as population growth is concerned, to surviving indefinitely and giving birth to n offspring at regular intervals. The hidden assumption that generated his apparent paradox has been revealed (Charnov and Schaffer, 1973), but Cole's definition of the theoretical problems attracted many workers, to the great benefit of the field.

Summary

By 1954, the main ideas of life-history theory were well defined. Subsequent effort has concentrated on the four areas reviewed below. We will see that people first broke life histories down into independent traits, and considered those in isolation. Recently, the process of reassembling tactics from sets of independent traits has begun. The areas to be reviewed are: (1) the argument over whether an organism should reproduce once or many times; the adaptive significance of variations in (2) clutch size, (3) age at first reproduction, and (4) size of young; and (5) the evolution of reproductive tactics as systems of coevolved adaptive traits.

THE NUMBER OF CLUTCHES IN A LIFETIME

A Paradoxical Result

Cole (1954) initiated a controversy with the following statement:

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 (p. 18).

He arrived at this conclusion on the basis of the following argument. Consider a population of annual organisms with no juvenile mortality, one that matures in the summer and dies after reproducing. When it has reached its stable growth rate, the following relationship holds:

$$N(t + 1) = e^r N(t) \\ = B_a N(t)$$

where B_a is the average female birth-rate per capita, and $N(t)$ and $N(t + 1)$ are population size in successive years. Thus,

$$\ln(B_a) = r.$$

Now consider an extreme case of iteroparity,

offering maximum growth, where the species produces B_p offspring per female every year starting at one year of age and continuing for eternity, with no mortality. Then we have

$$N(t + 1) = B_p N(t) + N(t) \\ = (B_p + 1) N(t)$$

and

$$\ln(B_p + 1) = r.$$

Thus, Cole concluded, if the annual and perennial populations are to increase at the same rate,

$$\ln(B_a) = r = \ln(B_p + 1),$$

or

$$B_a = B_p + 1.$$

The Controversy

Murdoch (1966) criticized Cole's conclusion on the grounds that the model that produced it assumed an oversimplified goal for organisms: maximizing growth rate. Whenever there is a trade-off between adult survival and reproductive effort, and the environment is variable, an adult that decides not to reproduce may have a better chance of surviving to the next breeding season than would the young produced if the adult had decided to breed. Gadgil and Bossert (1970) used the discrete form of Lotka's equation in attempting to analyze Cole's statement. They assumed that the population under consideration is not growing, that the females are just replacing themselves, and that although there is no mortality after maturity, there is juvenile mortality. Thus for an annual,

$$l_x b_x = l_1 b_1 = 1 \\ 1 = e^{-r} l_1 b_1 \\ r = \ln(l_1 b_1).$$

For a perennial species,

$$1 = \sum_1^{\infty} e^{-rx} l_x b_x dx = l_1 b_1 \sum_1^{\infty} e^{-rx},$$

which implies that

$$r = \ln(l_1 b_1 + 1), \text{ since } \sum_1^{\infty} e^{-rx} = \frac{1}{e^r - 1}.$$

Now since $l_1 b_1 \cong 1$, $r \cong \ln(2l_1 b_1)$. From this result, they modified Cole's statement to read:

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 (p. 11).

But surely this is nonsense, for the annual population is just replacing itself ($r = 0$), while the perennial population is growing quite rapidly ($r = \ln 2 = 0.69$). They are comparing apples and oranges. Their conclusion results from a rather free use of approximations and from setting $l_1 b_1 = 1$ for the perennials, when in fact their replacement assumption implies something quite different:

$$\sum_1^{\infty} l_x b_x = 1.$$

Bryant (1971) criticized Gadgil and Bossert for inducing a general result from a special case, and dealt with Lotka's equation by using a constant litter size, b , but an exponentially distributed survivorship, e^{-ux} , where u is the mortality rate:

$$1 = \sum_1^{\infty} e^{-(r+u)x}$$

which gives $r = \ln(b + 1) - u$, for the perennial. For an annual with the same pre-reproductive mortality as the perennial,

$$r = \ln(b) - u.$$

From this last expression, Bryant concluded that Cole's result was correct.

The Effects of Varying Age-Specific Mortality

Notice that Cole and Bryant both assumed equal adult and juvenile mortality rates (no mortality in either stage for Cole), whereas Gadgil and Bossert made the unnatural assumption of some juvenile mortality and no adult mortality. By examining variation in both adult and juvenile mortality, Charnov and Schaffer (1973) derived Cole's and Bryant's results as special cases. They compared two populations, one annual, the other perennial, producing B_a and B_p young per litter, respectively. The proportion of offspring surviving for the first year is C for both, while the perennials have an adult survival rate of P per year. Thus, the recurrence relations for population growth, given in terms of the number next year $N(t + 1)$, and the number this year, $N(t)$, are:

$$N(t + 1) = B_a \cdot C \cdot N(t)$$

for the annual, and

$$\begin{aligned} N(t + 1) &= B_p \cdot C \cdot N(t) + P \cdot N(t) \\ &= (B_p \cdot C + P) N(t) \end{aligned}$$

for the perennial. Thus

$$\lambda_a = B_a \cdot C, \quad \lambda_p = (B_p \cdot C + P),$$

and if the populations are to increase at the same rate,

$$B_a = B_p + (P/C).$$

In both Cole's and Bryant's models, $P = C$, giving

$$B_a = B_p + 1$$

which is Cole's result. Thus, Charnov and Schaffer restate Cole's result in this fashion:

For an annual species, the absolute gain in intrinsic population growth rate that can be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding P/C individuals to the average litter size (p. 792).

They also worked out the more complicated case of delayed reproduction.

Harper (1967), in examining the conditions under which the effective reproduction (recruitment of one-year-olds per female) of a biennial plant is equal to that of an annual, dealt with essentially the same ideas as Charnov and Schaffer, and made a similar prediction. But because he confounded the effects of delayed reproduction and the adult/juvenile survivorship ratio, and because he did not work with the characteristic equation, he failed to recognize the generality of his results. Both Murdoch (1966) and Cody (1971) recognized the importance of the adult/juvenile survivorship ratio for life-history tactics, and arrived at a less precise statement of the conclusions presented here.

To summarize the analysis made by Charnov and Schaffer: they emphasize the importance of separating juvenile and adult mortality. Age-specific mortality distributions play a large role in determining the optimal life-history tactic. Charnov and Schaffer predict that iteroparity will be favored, for both early and delayed reproduction, by adult survival rates which are high relative to juvenile survival rates.

The model used by Charnov and Schaffer exemplifies the implicit assumption that r is a phenotypic characteristic and that populations

consist of clones of asexually reproducing individuals. They have swept the complications of sex and genetics under the theoretical rug, and have chosen to base their conclusions on a very simple comparison of the effects of varying juvenile and adult mortalities. Although pure theoreticians might find these criticisms serious, they lose much of their strength when one recalls two points. No one has adequately dealt with the problems sex and genetics pose to a definition of fitness. I cannot fault Charnov and Schaffer, or others who use the same approach, for failing to solve a fundamental problem that has puzzled so many. Secondly, suppose their predictions, based on admittedly simplistic models, prove useful? Surely the proper grounds for rejecting a speculation that is logically sound within the limits of its assumptions are empirical. That Charnov and Schaffer chose to conceptualize life-history processes in a very simple model is not a valid criticism. If their predictions work, then perhaps complexity is not necessary. These comments apply equally to all the theoretical work, reviewed below, on *r*- and *K*-selection, age at first reproduction, and bet-hedging.

The Evidence

A direct test of the Charnov-Schaffer prediction would involve selection experiments on short-lived organisms, preferably in the field. Although such experiments have yet to be done, we can nevertheless gain some impression of the plausibility of the hypothesis through the analysis of published life tables. If the hypothesis is correct, then there should be a positive correlation between the average number of breeding seasons (a measure of "degree" of iteroparity) and the ratio of average juvenile to average adult mortality.

Let us define average number of breeding seasons as

$$\frac{\sum_{j=\alpha}^{\infty} n(j)(j - \alpha + 1)}{\sum_{j=\alpha}^{\infty} n(j)} \quad \text{for } b(j) \neq 0,$$

where α is age at first reproduction, $n(j)$ is the number of females in the cohort aged j , and $b(j)$ is the average number of female progeny born to females aged j . Define the

ratio of average juvenile mortality to average adult mortality as

$$\frac{\left[\sum_{j=0}^{\alpha-1} n(j)q(j) \right] / \left[\sum_{j=0}^{\alpha-1} n(j) \right]}{\left[\sum_{j=\alpha}^{\infty} n(j)q(j) \right] / \left[\sum_{j=\alpha}^{\infty} n(j) \right]}$$

where $q(j)$ is the probability of dying in the interval j to $j + 1$.

In examining the literature, I uncovered about fifty life tables, from which I selected twenty-three. I selected only life tables calculated from data gathered in the field on animals living in seasonal environments with a definite breeding season, with sample sizes larger than 150 animals, and where the authors did not confound mortality with migration or dispersal. There remain three possible problems with the tables selected: (1) there may have been inadequate replication, i.e. calculated from a single sample, or at a single place, or for a single year; (2) assumptions may have been made about the fecundity schedule, rather than estimations from measurements; or (3) there may have been perturbations of the population owing to human intervention, e.g., from fishing or hunting pressure.

The results are presented in Fig. 1 and Table 1. The table also notes which of the above three criticisms apply to each species. I have ranked the data and calculated Kendall's rank-correlation coefficient, tau. There is a strong enough correlation (tau = 0.26, $z = 1.78$, $p = 0.0375$) between the degree of iteroparity and the juvenile/adult mortality ratio to argue that a selection experiment would be worth doing. I certainly do not claim that the data in Table 1 reveal a "natural law." Problems in measurement make the data weak, there is considerable scatter, and I am sure that many forces other than mortality patterns have influenced the data. That we can only draw weak conclusions from the data available should spur more rigorous work.

Other Forces Selecting for Repeat Reproduction

Forces other than age-specific mortality also influence iteroparity. Holgate (1967) and Murphy (1968) pointed out that iteroparity will be directly selected for when the risk of total reproductive failure in any given year is signifi-

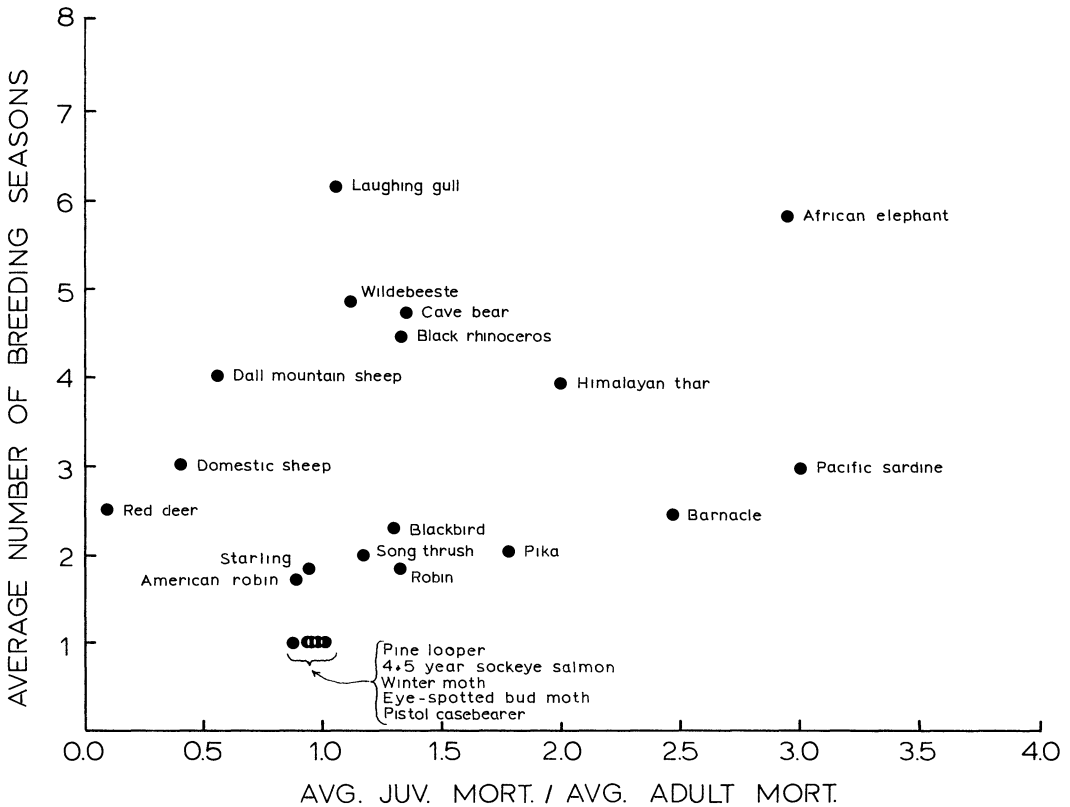


FIG. 1. EVIDENCE BEARING ON COLE'S PARADOX.

The average number of breeding seasons is positively correlated with the juvenile/adult mortality ratio. See Table 1 for references, text for explanation and criticism.

cant. Iteroparity may also arise concomitantly with parental care when post-reproductive survival is favored. Strathmann (1974), in considering the short-term advantages of large-scale dispersal of the sibling larvae of marine invertebrates, has suggested that iteroparity would promote dispersal by sampling a series of times and conditions for releasing planktonic larvae. Whenever larval dispersal is advantageous, he predicted more intense selection for iteroparity in species with shorter pelagic stages.

CLUTCH SIZE

The Hypotheses

There are at least five hypotheses on the evolution of clutch size. (1) The organism has as many young as it is physiologically capable

of producing. (2) Birds lay as many eggs as they can cover. (3) Organisms adjust the size of the clutch on the basis of information received through social mechanisms to balance the prevalent level of mortality and produce an "optimum" population size (Wynne-Edwards, 1962; Skutch, 1967). (4) Parents produce, on the average, the most productive clutch size, defined as that clutch size which results in the most young surviving to maturity. There is an optimum, or most productive, clutch size corresponding to any particular set of ecological conditions, and it is determined primarily by the amount of food the parents are capable of bringing to the young (Lack, 1947, 1948, 1954). (5) Clutch size is determined by a balance of allocations of limited resources to competition, predator avoidance, and reproduction (Cody, 1966). A sixth point of view places clutch size in a more comprehensive context. It is

TABLE 1
A comparison of mortality ratios and breeding seasons

COMMON NAME	SCIENTIFIC NAME	J/A MORT.	NO. SEAS.	REFERENCE	CRITICISM (see text)
Red Deer	<i>Cervus elephas</i>	0.092	2.4874	Lowe, 1969	1,3
Dall Mountain Sheep	<i>Ovis d. dalli</i>	0.554	4.0109	Deevey, 1947; Geist, 1971	1
Himalayan Thar	<i>Hemitragus jemlahicus</i>	1.995	3.9209	Caughley, 1966	1,3
Wildebeeste	<i>Connochaetes taurinus</i>	1.120	4.8380	Watson, 1970	1
American Robin	<i>Turdus m. migratorius</i>	0.888	1.6899	Deevey, 1947; Lack, 1954	1,2
Starling	<i>Sternus vulgaris</i>	0.939	1.8443	Deevey, 1947; Lack, 1954	1,2
Robin	<i>Eriothacus rubicula</i>	1.315	1.8234	Deevey, 1947; Lack, 1954	1,2
Song Thrush	<i>Turdus ericetorum</i>	1.168	1.9861	Deevey, 1947; Lack, 1954	1,2
Blackbird	<i>Turdus merula</i>	1.294	2.2750	Deevey, 1947; Lack, 1954	1,2
Laughing Gull	<i>Larus argentatus</i>	1.056	6.1615	Kadlec & Drury, 1968	2
Barnacle	<i>Balanus glandula</i>	2.468	2.4575	Connell, 1970	2
Pika	<i>Ochotona princeps</i>	1.780	2.0276	Millar & Zwickel, 1972	1,2
Black Rhinoceros	<i>Diceros bicornis</i>	1.324	4.4553	Goddard, 1970	1,3
Pine Looper	<i>Bupalus piniarius</i>	0.977	1.0000	Klomp, 1966	3
Four-Year Sockeye Salmon	<i>Onchorhynchus nerka</i>	0.982	1.0000	Hanamura, 1966	2,3
Five-Year Sockeye Salmon	<i>O. nerka</i>	0.976	1.0000	Hanamura, 1966	2,3
Domestic Sheep	<i>Ovis aries</i>	0.398	3.0181	Hickey, 1960	1,3
Cinnabar Moth	<i>Tyrea jacobaeae</i>	0.987	1.0000	Dempster, 1971	3
Pacific Sardine	<i>Sardinops caerulea</i>	3.007	2.9575	Murphy, 1967	2,3
Winter Moth	<i>Operophtera brumata</i>	0.996	1.0000	Embree, 1965	1,3
Diamondback Moth	<i>Plutella maculipennis</i>	0.933	1.0000	Harcourt, 1963	3
Eye-Spotted Bud Moth	<i>Spilonota coellata</i>	0.972	1.0000	LeRoux, Paradis, & Hudon, 1963	3
Pistol Casebearer	<i>Coleophora serratella</i>	0.870	1.0000	LeRoux, Paradis, & Hudon, 1963	3
African Elephant	<i>Loxodonta africana</i>	2.951	5.8162	Petrides & Swank, 1966	1,2

discussed below under the heading of, "Reproductive Tactics."

The first and second hypotheses are at best special cases, for they are contradicted by the evidence (Lack, 1948, 1954; Cody, 1966, 1971; Klomp, 1970). Wynne-Edward's hypothesis requires group selection, which may or may not occur in nature. But group selection would only rarely overcome individual selection (cf. Levins, 1970; Wilson, 1973), and in any case should be invoked only when individual selection cannot account for the phenomena observed (Williams, 1966a). However, much of the evidence adduced by Wynne-Edwards and Skutch in arguing against Lack's hypothesis needs explanation, and may have found it in the theories of reproductive tactics. Lack's hypothesis that clutch size is adjusted to maximize the number of young fledged held the field for about fifteen years (1950-1965), still has many adherents

among ornithologists, but has been subsumed, with modifications, in a more comprehensive theory. In this section I shall discuss some criticisms of Lack's hypothesis, review Cody's early ideas on clutch size (Cody, 1966), and then present three recent models that predict clutch sizes smaller than the one that fledges the most young.

Problems with Maximizing Productivity

There are two aspects to Lack's hypothesis that are best kept separate. On the one hand, Lack proposed that, within a population in a single geographical location, the average clutch size will be the one that fledges the most young, as a result of selection. On the other hand, Lack explained the known geographical trend toward larger clutches at higher latitudes as the result of longer daylengths that allow

parents more time to get food and thus increase the size of the most productive clutch.

There is some evidence that birds do tend to produce a clutch near the most productive of the clutch sizes available to them. Klomp (1970), in an exhaustive review of clutch size in birds, concluded that evidence from the six well-studied species supports Lack's hypothesis. Where there are discrepancies, the most frequent clutch size is smaller than the one that fledges the most young (four well-studied species), except for the Common Heron. Several models, reviewed below (p. 15 ff.), suggest ultimate factors that favor reduced clutch sizes.

Drury (1961) studied the biology of passerines in the Canadian Arctic. He noted that, although there were significant differences in clutch size between the southern and northern parts of the bird's range, the southern populations, with a clutch size of 4 to 5 eggs, had enough available daylight (20 hours) to feed a clutch size as large as the ones that northern populations raised (6 to 7 eggs). Drury suggested that the larger clutch sizes in the north could be explained (1) as adaptations to increased r , allowing for rapid recovery from disasters induced by climatic extremes; and (2) as the result of concentrating the annual production of young into one, rather than two, successive clutches, and thus allowing equivalent production over the shorter arctic summer.

On the other hand, Hussell (1972), in a more exhaustive field study of arctic passerines, sought evidence that the increase in clutch size with latitude was related to the day-length available for food collection. He found that variation in clutch size with latitude, as well as with other factors, was related to environmental factors influencing the food-gathering potential of parents.

Two older theories on clutch size should be considered. One can be disposed of easily. Wynne-Edwards (1962) argued against Lack on the basis of the existence of broad negative correlations of clutch size with population density in birds and mammals. Wynne-Edwards explained these correlations by the infamous theory (cf. Williams, 1966a) that through social interactions the animals notice they are approaching critical density and self-regulate their population density by reducing clutch size to prevent a population crash. Group selection is required for the evolution of this type of be-

havior, since if only individual selection is operating, the individual who "cheats" and has a large clutch will win out. Since group selection probably rarely occurs, and when present is less efficient than individual selection in changing gene frequencies, we may disregard Wynne-Edwards's theory. If clutch size decreases over evolutionary time as population density increases, it probably does so because selection acts on individuals under such circumstances to favor small clutches, for any of a large number of reasons reviewed below and in the section on r - and K -selection and bet-hedging.

Skutch's (1949, 1967) ideas are less easily disposed of. He maintained that under stable conditions populations are operating at close to saturation density most of the time. Under these conditions (e.g., in the humid tropics) there is no point in raising as many young as you can feed, since all those beyond the number needed for replacement will die. Skutch suggested that, instead, clutch size is adjusted to balance mortality under saturation conditions. In countering Lack's food-limitation argument, he cited several cases of two species of birds of the same genus, living in the same habitat, that raise the same clutch size to maturity even though both parents feed the young in one species, and only one parent in the other. In countering Lack's most-productive-clutch hypothesis, he cited the advantages that small clutch sizes may have in reducing the risk of predation to parents and young: fewer visits to the nest are required, and that decreases the chance of the nest being found. Furthermore, in those species Skutch cited as evidence, the young do not give begging calls, and the food items brought to the nest are quite large, a condition which further reduces the necessity for repeated feeding flights and decreases the probability of detection by predators.

Ricklefs (1969) stated as a generality that predation is the major cause of death for eggs and nestling birds, regardless of geographical location, habitat, or nest site, and that starvation is less frequently a source of mortality in the humid tropics. This generalization lends support to Skutch's emphasis on the problems encountered by nesting birds in dealing with predators. Fretwell (1969) has suggested that the hypotheses of Lack and Skutch can be reconciled by supposing that adults try to pro-

duce as many breeding offspring as they can, but that wherever mortality selectively impinges on excess offspring through social dominance or other effects, then the birth-rate can be adjusted downward, not in order to balance the death-rate, but to maximize the number of surviving progeny.

Skutch's explanations of lower clutch sizes in the tropics are not the only ones. One alternative explanation is that where replacement is important, a few high-quality young are preferable to many low-quality young, as has been suggested for fish by Svardson (1949) and Williams (1966a). In fact, a bet-hedger would produce just a few more high-quality young than are necessary for replacement, in order to take advantage of occasional fluctuations in conditions to increase the number of surviving young. The number of additional young produced will depend on the probability of a change in conditions.

Much of the argument over Lack's hypotheses has stemmed from misinterpretations of Lack's intent, from his overly strong insistence on food as the proximal limit on clutch size, and from the fact that in the 1950's and 1960's, when the argument was at its peak, the concept of a tradeoff between reproductive effort and parental survival had not entered the discussion. I am sure Lack was on the right track in saying that birds produce clutch sizes that leave the most survivors. The only real changes in our thinking about clutch size have come, first, in how we count survivors—not just fledglings from a single clutch but all young produced over the life span of the parent; secondly, in recognizing that factors other than food, such as predation or parental survival, may be limiting in many cases; and thirdly, in recognizing that an alternative explanation arises when we ask not how to maximize the number of young produced, but how to minimize the probability of leaving no young at all.

A Trade-Off Model

Restating much of what Skutch had said, Cody (1966) reasoned that organisms have a limited amount of energy, and that they allocate it to reproduction, competition, and avoidance of predation. Energy not needed for competition can go into reproduction, and so forth: there are trade-offs among the three state

variables. It is difficult to see how an animal's ability to compete or to avoid predators could be a simple function of energy allocation. Morphological design seems to me more important.

Nevertheless, Cody predicted that in environments he defined as unstable (temperate, arctic) most energy will go into increasing the reproductive rate, and thus increasing clutch size, at least in part. In environments he defined as stable (the tropics, islands, coastlines), we should find smaller clutches. Finally, hole-nesting species, which are relatively predator-free, but more so in the tropics than in the temperate areas, should have larger clutches in all areas, but would exhibit less of an increase of clutch size with latitude. All of Cody's predictions were corroborated by the data he cited, but I question his definitions of stability and instability. We have few, if any, good data on how stable different environments appear to organisms. Without an independent measure of stability, Cody's argument is circular. Nor did he consider alternative explanations, which exist in abundance (cf. Table 5).

Models Favoring Small Clutches

Cody predicted clutch sizes smaller than the most productive clutch size on the basis of a trade-off between reproduction, competition, and predator avoidance. There are at least three other theoretical models that predict clutch sizes smaller than the most productive. In that sense, all three offer modifications to Lack's hypothesis.

The first, developed by Charnov and Krebs (1973) and based on the central idea in Williams (1966b), makes the assumption that there is a positive correlation between clutch size and adult mortality. They argued that for a perennial species, where the act of reproduction implies a mortality risk, large clutch sizes reduce the parents's chances to survive and reproduce in the future. The lifetime contribution to future generations is optimized by producing clutches smaller than the most productive single clutch (Fig. 2). Table 2 cites evidence that there is a trade-off between reproduction and adult mortality. However, this prediction depends to a certain degree on the shape of the trade-off function, which has never been measured in any species. Its measurement will be one step

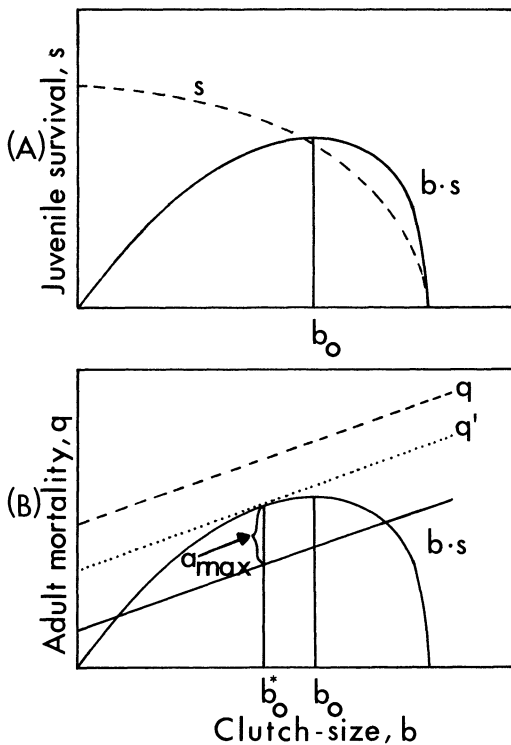


FIG. 2. A GRAPHICAL ARGUMENT ON OPTIMIZING CLUTCH SIZE

(A) The relationship between clutch size, b , and survival rate for the first year of life, s (broken line). The resulting $b \cdot s$ or production curve (solid line) has a single maximum at b_0 . Under Lack's hypothesis this is the clutch favored by natural selection.

(B) The impact of the cost of reproduction. If adult mortality, q (dashed line), increases with b , then the clutch b_0^* that maximizes the measure of fitness, a , is always smaller than b_0 . The optimal clutch is found by constructing the line parallel to q (q' , dotted line) which just intersects the $b \cdot s$ curve (solid line). In general, clutches smaller than b_0 will have a higher fitness than those larger.

in testing both this and other theories on life history phenomena (cf. Williams 1966a, b; Schaffer, 1972, 1974a).

The second modification, suggested by Cohen (1967) and by Boer (1968) but most thoroughly developed by Mountford (1973), involves the idea of hedging bets in the face of uncertainty. Suppose environmental conditions vary from year to year, and that the organism cannot be certain, at the time of

reproduction, what conditions will be like for the rest of the year. Since making too large a reproductive effort may result in disaster (with all the young and perhaps the parents dying) whereas laying a less than optimal clutch at least results in some young, the organism should always hedge its bet on the side of a smaller than optimal clutch, rather than in the other direction (Fig. 3). Mountford (1968) described an alternative mechanism that produces the same result. If one assumes that organisms produce a normal distribution of clutch sizes over their lifetime, and that the proportion recruited decreases with clutch size, then compares a series of similarly shaped distributions of clutch size that have different means, one discovers that the distribution that produces the most recruits over the organism's lifetime has a mode that is less than the most productive single clutch.

Mountford (1973) emphasized that if the goal is to minimize the probability of extinction, then the tactics selected will usually differ from those based on the traditional criterion of maximizing growth rate. His model deals with populations, not individuals, as the units of selection. In general, there are good biological reasons not to do this: selection acts on individuals, not on groups. But under special circumstances, the idea becomes more plausible and brings up the third argument, put forth by Gilbert and Gutierrez (1973). They dealt with a population broken up into groups, each of which undergoes independent growth and eventual density-dependent limitation. Under these special circumstances, how can the organism avoid selection for ever-increasing fecundity, which would greatly increase the chances of group extinction? They point out that the total fitness of an individual over the entire growing season is made up of two factors, its fecundity during the growth phase and its contribution to group fecundity during the density-limited phase. Individual selection will act to maximize total fitness. When there is a correlation between group fecundity and probability of extinction, optimum individual fecundity is less than the most productive individual fecundity. This model works for an aphid population, where the members of groups are closely related, but for sexually outcrossing organisms the situation changes, and "cheaters" may win.

TABLE 2

Evidence that there is a real cost associated with reproducing

TYPES OF EVIDENCE	SPECIES	REFERENCE
(1) Increase in adult mortality during and after reproduction: relative to those that do not reproduce	Rocky Mountain Sheep: <i>Ovis dalli</i>	Geist, 1971
	carabid beetles: <i>Agonum</i> spp.	Murdoch, 1966
	littoral gastropods	Fotheringham, 1971
	<i>Shaskyus</i> and <i>Ocenebra</i> spp.	
	house sparrow: <i>Passer domesticus</i>	Summer-Smith, 1956
	European blackbird: <i>Turdus merula</i>	Snow, 1958
	isopod: <i>Armadillidium vulgare</i>	Paris & Pitelka, 1962
	meadow voles: <i>Microtus agrestis</i>	Clouch, 1965
	pandalid shrimp: <i>Pandalus borealis</i>	Allen, 1959
	Olive Baboon: <i>Papio anubis</i>	Berger, 1972
(2) A decrease in growth rate during and after reproduction: relative to those that do not reproduce	minnow: <i>Pimephales promelas</i>	Markus, 1934*
	bug: <i>Dysdercus fasciatus</i>	Clark & Sardesai, 1959*
	barnacles: <i>Elimnius modanus</i>	Crisp & Patel, 1961
	<i>Balanus balanoides</i>	Barnes, 1962
(3) A reduction in reproductive effort, or an increase in sterility or infertility in underfed animals.	sugar cane: <i>Saccharum officinarum</i>	
	guinea pig	Loeb, 1917
	sheep and cows	Hammond, 1958*
	pigs	Lamming, 1969*
	domestic fowl	Duncan & Lodge, 1960*
	rainbow trout: <i>Salmo gairdneri</i>	Brody, 1945; Peterson et al., 1960; Kurnick et al., 1961
		Scott, 1962

*cited in Calow, 1973

Summary

Lack's original hypothesis has been reinterpreted in later models that alter it without destroying it. In the process, emphasis has shifted to a different way of looking at the evolution of life-history traits. Instead of isolating one adaptive trait and looking for the ecological interactions that determine its observed variation, we must consider organisms as systems of interacting, coadapted traits, with trade-offs among them. As Hussell put it,

... a distinction should be made between the factors responsible for the short-term regulation of populations and those responsible for the long-term evolution of reproductive rates and the other aspects of the life cycle. In the short term birds are probably reproducing as rapidly as possible within the limits set by their current genetically controlled capabilities. Population sizes would then be regulated by subsequent density-dependent mortality. But the idea of maximization of the reproductive rate, in relation to the environmental food supply has no meaning in the context of

the evolutionary processes involved. Natural selection does not operate to maximize the reproductive rate, but favors those characteristics which allow the individuals possessing them to maximize their overall genetic contribution to subsequent breeding populations. This can be achieved by changes in any aspect of the reproductive strategy (Hussell 1972, p. 353).

At least five theoretical models incorporate mechanisms that account for the reduction of clutch size below the most productive size: (1) trade-offs between demands for resources on the part of reproduction versus other functions (Cody, 1966; Skutch, 1967); (2) trade-offs between clutch size and adult mortality (Charnov and Krebs, 1973); (3) bet-hedging in the face of uncertainty about conditions during the breeding season (Boer, 1968; Holgate, 1967); (4) the interaction of a normal distribution of clutch sizes with a probability of recruitment that declines with increasing clutch size (Mountford, 1968); and (5) a positive correlation between clutch size and the probability of

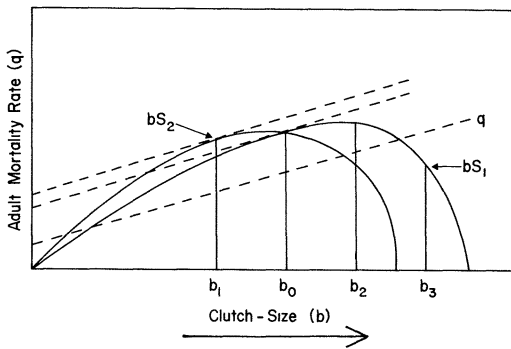


FIG. 3. BET-HEDGING REDUCES AVERAGE OPTIMUM CLUTCH SIZE

Assume again, as in Fig. 2, a trade-off between clutch size and survival of young. Define symbols as in Fig. 2. If there is year-to-year variability in the optimal clutch size, selection favors bet-hedging with a smaller clutch. Let b_0 be the optimal clutch size this year, with $b \cdot s$ curve 1. If in the next year changed conditions result in $b \cdot s$ curve 2, then a smaller clutch, b_1 , will offer maximum fitness, while an equivalently larger clutch, b_2 , offers much reduced fitness; a very large clutch, b_3 , would result in a serious mortality risk to the parent and no young at all. The analysis given depends on the shape of the $b \cdot s$ and q curves, which certainly vary from species to species, place to place, and time to time.

extinction where the population is broken up into groups of closely related organisms (Gilbert and Gutierrez, 1973).

AGE AT FIRST REPRODUCTION

Cole (1954) and Lewontin (1965), among others, have pointed out that, in a growing population, selection will push the age at first reproduction to the physiological minimum. This can perhaps best be seen by analogy with compound interest in banking: it will always pay to get your money in the bank as soon as possible so that the compounding interest rate will get to work most rapidly.

More specifically, Cole (1954: Figs. 4 and 5) pointed out that, other things being equal, the advantage of a lower age at first reproduction is greater for animals with large clutch sizes than for those with small ones, and greater for semelparous than for iteroparous organisms. Lewontin (1965) used a simulation model to deal with the sensitivity of the population

growth rate, r , to changes in the age at first reproduction, the age at which reproductive value starts to decline (the turnover point), and the age at last reproduction. He found that r was most sensitive to a decrease in age at first reproduction, less sensitive to an equivalent decrease in the turnover point, and quite insensitive to a decrease in the age at last reproduction (holding total number of progeny constant in all cases). Decreasing the age at first reproduction from 12 to 9.8 days was equivalent to doubling the total number of progeny produced.

On the other hand, Hamilton (1966) noted that, during a population decline, the individual should delay reproduction to the modal age of the stable age distribution in order to slow the rate of decline. Mertz (1971a, b) made the same point, and suggested that the delayed reproduction and longevity of the California condor may represent an adaptive response to a long period of decline in size of population.

Mertz suggested that populations which experience long periods of decline punctuated by brief episodes of expansion will evolve delayed reproduction, but offered no method of quantifying the prediction. According to models of island populations proposed by MacArthur and Wilson (1967), a colonizing species multiplies rapidly in a new habitat, then declines slowly. During the decline it sends off propagules to other habitats. According to Mertz, such populations should delay reproduction, but according to MacArthur and Wilson, Lewontin, and others, they should have early reproduction. (I thank G. C. Williams for pointing this out to me.)

The different predictions stem from different estimates of the frequency of colonizing episodes. We need a comprehensive theoretical treatment of the impact of different frequencies of colonizing episodes on the evolution of life-history tactics. Such an analysis should reveal a critical region in the frequency of colonization below which early reproduction is favored, and above which delayed reproduction is favored, given a declining population. Another analogy with banking is useful here. If the interest rate is positive, it pays to get your money in the bank as soon as possible. When the bank, instead of giving interest, levies a monthly charge on money deposited, but you know you eventually must deposit the money, then it pays to delay

putting your money in the bank as long as possible.

In fact, population growth rates fluctuate around zero. Rarely will a population experience a long, uninterrupted period of increase or decline. Thus pure r -selection, or pure selection for delayed reproduction as proposed by Hamilton and Mertz, represent unrealistic theoretical limiting cases rarely approached in nature. When the growth rate is confined to a narrow band around zero, I expect entirely different selection forces to dominate.

Other authors have discussed factors which favor delaying the age at first reproduction, e.g., Harper (1967), Murphy (1968), Gadgil and Bossert (1970), Cody (1971), Geist (1971), Schaffer (1972), Schaffer and Reed (1972), and Schaffer and Elson (1975). Some of these will be discussed in more detail in the section on reproductive tactics (below). They may be summarized as follows. (1) If juvenile survival is greater than adult survival (because juveniles live in a protected habitat, or because there is a significant trade-off between reproduction and adult survival), then it is advantageous to delay reproduction to a certain point. Healy (1974) has documented reproductive trends in Massachusetts newts (*Notophthalmus*) that support this view. (2) If reproductive success depends on age, size, or social status, as it does in many hierarchical societies (e.g., mountain sheep, baboons, and seals) and in species where it takes considerable effort just to reproduce at all (e.g., salmon and eels), then delayed maturity will again be favored.

REPRODUCTIVE TACTICS

So far we have been considering different aspects of a life history as more or less isolated and independent phenomena. Now let us put them together as a system of interrelated adaptive traits forming a set of reproductive tactics. There are at least four different viewpoints in the literature on how to look at reproductive tactics. How sensitive are fitness measures to changes in different parameters of a life history? How do r - and K -selection and bet-hedging affect life histories? How do life histories evolve in variable environments? And how do trade-offs between reproductive effort and other commitments affect life histories? These four

viewpoints on reproductive tactics overlap and interpenetrate extensively.

Fitness As A Function of Life History Traits

The characteristics of a population have evolved together as interrelated traits. Evolutionary changes in one trait may imply compensatory or opportunistic changes in another trait. The most revealing question to ask of such a system is this: How sensitive is fitness to a change in any one of the traits? Is this sensitivity itself a function of the other traits? We may consider as most important that trait to whose change fitness is most sensitive. Given that we are willing to accept a single fitness measure as appropriate, we may rank the importance of any set of traits whose relationship to a given fitness measure can be precisely expressed. Cole (1954), Lewontin (1965), and Meats (1971) have used this procedure to explore the sensitivity of rate of increase (R_0 or r) to changes in life history parameters.

Cole (1954) found that r is quite sensitive to changes in age at first reproduction (A), and that r is much more sensitive to a given percentage change in A when A is low. Moreover, r is much more sensitive to a change in A when the birth-rate is high. Thus, one could expect to find age at first reproduction and birth rate under strong selection when populations are growing rapidly.

Lewontin (1965) was concerned with those combinations of life history traits that produced individuals fit for colonization. He assumed exponential population growth, a stable age distribution, and overlapping generations, and took r as his fitness measure. He then modeled a life history using $V(x) = l_x b_x$ as a triangular function of age x (see Fig. 4), and defined A , T , and W as age at first reproduction, age at peak reproduction, and age at last reproduction, respectively. To derive an expression for r in terms of these parameters, Lewontin noted from the geometry of Fig. 4 that

$$V(x) = \frac{2S(W-x)}{(W-T)(W-A)}, x \geq T$$

$$V(x) = \frac{2S(x-A)}{(T-A)(W-A)}, x < T$$

He then substituted these expressions in

$$1 = \int_0^{\infty} e^{-rx} V(x) dx$$

integrated, and obtained a complicated implicit expression for r that could be evaluated numerically.

He took as his baseline the case where $A = 12$ (age at first reproduction), $T = 23$ (age at peak reproduction), $W = 55$ (age at last reproduction), $r = 0.30$, and $S = 780$ (total eggs expected per female over her lifetime). The change in S required to change r from 0.30 to 0.33 is +670, nearly a doubling to 1350 eggs. The changes in the other parameters that would be equivalent in effect on r to this change in fecundity are a 1.55 unit rigid translation of the $V(x)$ triangle to the left, a 2.20 unit decrease in age at first reproduction, a 5.55 unit decrease in age at peak reproduction, and a 21.00 unit decrease in age at last reproduction. r is most sensitive to a given change in units of time when fertility is high and age at first reproduction low, and is least sensitive when fertility is low and age at first reproduction high, as Cole found. But, in general, r is most sensitive to changes in age at first reproduction. From this, Lewontin predicted that colonizing

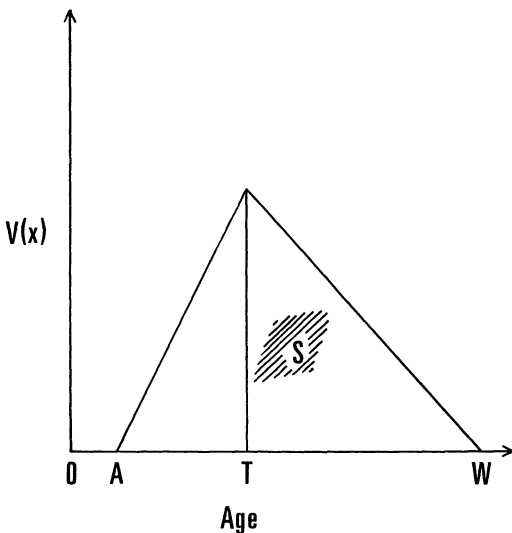


FIG. 4. LEWONTIN'S MODEL OF A LIFE HISTORY

$V(x) = l_x b_x$ is, in general, triangular. A , age at maturity; T , turnover point; W , age of last reproduction; S , total number of offspring; x , age; l_x , probability of surviving to age x ; b_x , average number of young produced by a female age x . (After Lewontin, 1965.)

species should show much less genetic variance in age at first reproduction, which is under strong selection pressure, than they show for fecundity.

Meats (1971) extended Lewontin's analysis to a wider range of values of r and examined the separate effects of M and N , mortality and natality, for both discrete and overlapping generations. He found that when prereproductive mortality is high (ca. 0.80–0.99), the growth rate of an annual population (R_0) is much more sensitive to changes in mortality than natality; when juvenile mortality is low (ca. 0.01–0.60), the effects of a given percentage change in mortality or natality are nearly equivalent. Using Lewontin's example as a baseline, he found that as r declines below 0.05, it becomes less sensitive to changes in age at first reproduction (A), peak reproduction (T), and last reproduction (W). When r drops below about 0.025 in Meats' model it becomes more sensitive to changes in birth-rate than to age at first reproduction. r shifts sensitivity from T to birth-rate at about 0.030, and from W to birth-rate at about .050. Thus, at low values of r , Lewontin's results are qualified or reversed.

r- and K-Selection, or Bet-Hedging?

Since life-history traits are intimately interrelated, attempts to explain variability in life-history traits should model the important traits and their interactions. Two theoretical approaches have begun this process. They have led to contradictory predictions. One approach travels under the name "*r- and K-selection*"; I call the other approach "*bet-hedging*." Advocates of *r- and K-selection* deal with models in which mortality and fecundity schedules do not fluctuate. Advocates of *bet-hedging* try to deal with the consequences of just such fluctuations.

r- and K-Selection

The idea of *r- and K-selection* originated with Dobzhansky (1950), who proposed that natural selection operates in a fundamentally different way in the tropics than it does in temperate areas. He argued that in temperate areas physical factors are most frequently limiting. These act in density-independent fashion, selecting for lower age at first reproduction and larger clutches (Schmalhausen, 1949). But, he argued,

in tropical areas biological interactions predominate, leading to selection for ability to compete and to avoid predation. Skutch (1949, 1967) has made similar suggestions. MacArthur (1962) gave theoretical support to these ideas by deducing that, in density-dependent situations, natural selection will favor genes that have a higher carrying capacity, K , and by suggesting that in such situations K can replace r , the Malthusian parameter, as a fitness measure. On the other hand, Lewontin (1965) emphasized that in colonizing situations (where limitation tends to be density-independent) age both at first reproduction and at the turnover point in reproductive effort should be minimized, and the clutch size increased, in that order.

MacArthur and Wilson (1967) drew these ideas together and coined the terms " r -selection" for selection in environments favoring rapid population growth, and " K -selection" for selection in saturated environments, favoring ability to compete and to avoid predation. Their discussion provoked the spurt of papers published on the topic in the last five years (Pianka, 1970, 1972; King and Anderson, 1971; Roughgarden, 1971; Hairston, Tinkle, and Wilbur, 1970; Cody, 1971; Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973).

Table 3 summarizes the correlates of r and K -selection in the environment and in the organism (modified according to Pianka, 1970). Most of the relationships follow in a straightforward fashion from the arguments given by Schmalhausen and Dobzhansky, or are outlined above where I considered the traits one at a time. The theory is qualitative, not quantitative, and admits comparisons only within limited groupings. But it does predict the association of the biological traits constituting life-history tactics into two groups: (1) r -selection: early age at first reproduction; large clutch size; semelparity; no parental care; a large reproductive effort; small, numerous, offspring; low assimilation efficiency; and a short generation time; (2) K -selection: delayed reproduction; iteroparity; small clutches; parental care; smaller reproductive effort; a few, large offspring; and high assimilation efficiency.

Bet-Hedging

Murphy (1968) and Schaffer (1974b), who examined the same trends from the bet-hedging

viewpoint, generated markedly different predictions. Murphy compared two populations in a computer simulation. Population 1 ($r = 0.3188$, $\alpha = 3$) had later age at first reproduction, better adult survival rates, lower fecundity, and a higher carrying capacity than Population 2 ($r = 0.5472$, $\alpha = 2$). The two populations were linked by Ricker's (1954) reproductive equations. When the interaction coefficients were equal and there was no environmental variability, the simulation model behaved realistically. Population 2 (short-lived, high r) increased more rapidly than Population 1 (long-lived, lower r), then went extinct as Population 1 grew past the carrying capacity of Population 2. Next Murphy altered the interaction coefficients so that the two populations coexisted in a stable environment (Pop. 1 = 2364 individuals, Pop. 2 = 6757 individuals). He started both populations with 1000 individuals. Then after 26 time units, when they had almost reached equilibrium, he introduced uniform random variation in reproductive success. In all cases, Population 1 increased in numbers and dominated, while Population 2 decreased in numbers, but did not go extinct (Fig. 5).

This result goes counter to the r -selection argument, but seems to be supported by data on herring-like fish, whose reproductive span is strongly correlated with variation in spawning success (Murphy, 1968). Murphy's ideas are quite similar to those presented in Fig. 3, a resemblance which argues that environmental variability selects for reduced clutch size, and his data suggest that the effect could be quite strong. Note that variation in reproductive success is essentially synonymous with variation in juvenile mortality.

Schaffer (1974b) extended and reinforced Murphy's conclusions with a simple population model. Consider a population without age structure. Then

$$\lambda = B + P$$

where B is the number of offspring that survive from time t to time $t + 1$, and P is the probability that the female herself survives to breed again. Both B and P are functions of reproductive effort, E . In a fluctuating environment, breeding success and adult survival vary from year to year. In such circumstances, the long-term rate at which a population increases, $\bar{\lambda}$, is the

TABLE 3
Some of the correlates of *r*- and *K*-selection

	<i>r</i> -SELECTION	<i>K</i> -SELECTION	REFERENCE
Climate	Variable and/or unpredictable	Constant and/or predictable	Dobzhansky, 1950; Skutch, 1949, 1967; Pianka, 1970; MacArthur & Wilson, 1967
Mortality	Density-independent; uncertain adult survival	Density-dependent; uncertain juvenile survival	Pianka, 1970; Murphy, 1968; Cody, 1971
Survivorship	Often Type III (Deevey, 1947)	Usually Types I and II (Deevey, 1947)	Pianka, 1970
Population size	Variable in time, nonequilibrium; usually below carrying capacity; frequent recolonization necessary	Constant in time, equilibrium; at or near carrying capacity; no recolonization necessary	MacArthur & Wilson, 1967; Pianka, 1970
Competition	Often lax	Usually keen	Dobzhansky, 1950; Skutch, 1967; MacArthur & Wilson, 1967
Selection favors	<ol style="list-style-type: none"> 1. Rapid development 2. High <i>r</i>-max 3. Early reproduction 4. High resource thresholds 5. Small body size 6. Semelparity 7. Increased birth rate 	<ol style="list-style-type: none"> 1. Slow development 2. Competitive ability 3. Delayed reproduction 4. Low resource thresholds 5. Large body size 6. Iteroparity 7. Decreased death rate 	<p>Schmaulhausen, 1949; Dobzhansky, 1950; Cole, 1954; Lewontin, 1965; MacArthur & Wilson, 1967; Gadgil & Bossert, 1970; Pianka, 1970; Hairston, Tinkle, & Wilber, 1970; Meats, 1971</p>

Length of life	Short, <1 year	Long, >1 year	King, 1964; Pianka, 1970
Leads to	Productivity	Efficiency	MacArthur & Wilson, 1967
Proportion of energy allocated to reproduction:	Relatively large	Relatively small	Gadgil and Solbrig, 1972
1. Mass of offspring/parent/brood;	Larger	Smaller	
2. Mass of offspring/parent/lifetime;	Larger	Smaller	
3. Size of offspring;	Smaller	Larger	
4. Parental care	Less	More	
Coarse-grained seasonal environments lead to a stable polymorphism between high <i>r</i> - and high <i>K</i> -genes Roughgarden, 1971			
Number of breeding periods per seasonal cycle	Fewer	More	King & Anderson, 1971
Tolerance to niche overlap	Larger	Smaller	Pianka, 1972
Degree of polymorphism of genes determining carrying capacity and niche breadth	Less	Greater	Clarke, 1972

(modified after Pianka, 1970)

SUMMARY OF MURPHY'S MODEL

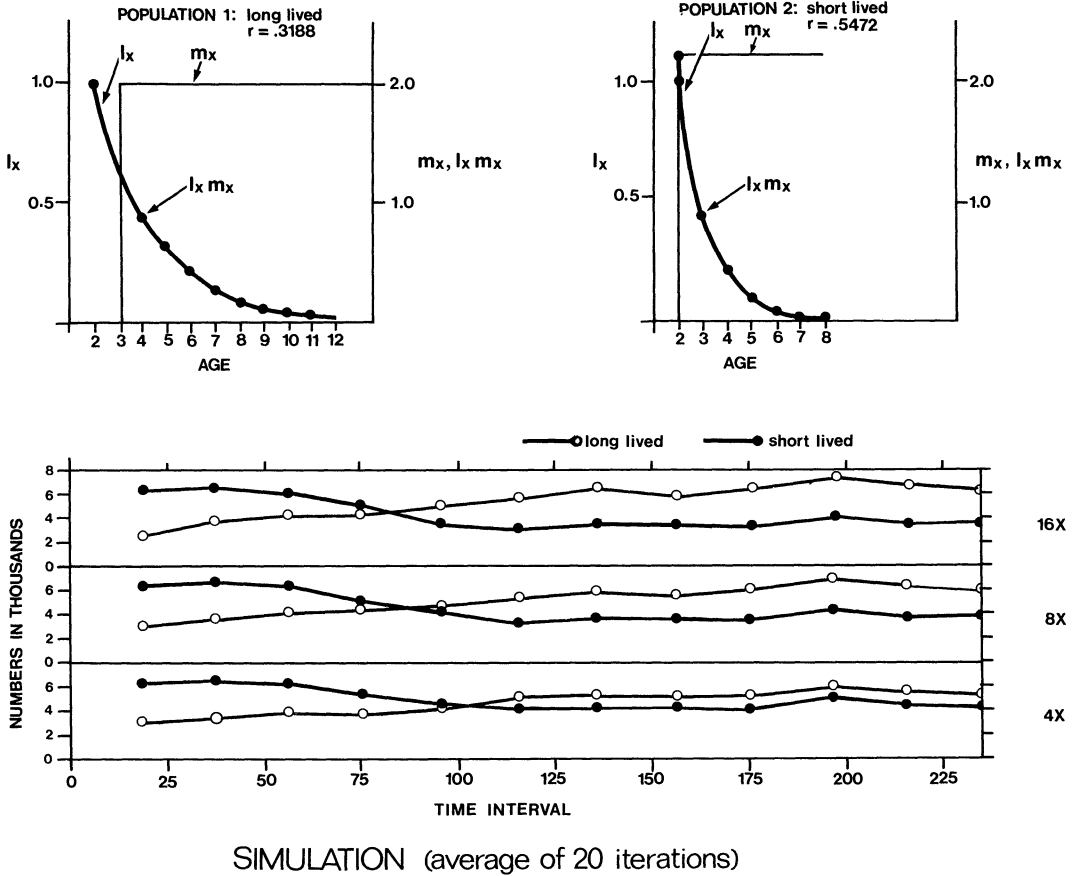


FIG. 5. THE IMPACT OF VARIATIONS IN RECRUITMENT ON LIFE HISTORIES

Simulation of the impact of random variation in reproductive success (juvenile mortality) on a long-lived, slowly growing population, compared with a short-lived, rapidly growing population. At all three levels of variation in reproductive success (4x, 8x, and 16x), the long-lived population becomes dominant about 75 time-intervals after the introduction of variability at the 26th time-interval. (Adapted from Murphy, 1968).

product of the various rates of increase in different environments (e_1, e_2, \dots, e_n), raised to a power q_i equal to the frequency of the environment. Therefore,

$$\bar{\lambda} = \lambda_1^{q_1} \lambda_2^{q_2} \lambda_3^{q_3} \dots$$

and

$$\ln(\bar{\lambda}) = \sum_1^{\infty} q_i \ln(\lambda_i) \quad (\text{Levins, 1968}).$$

Schaffer considered the simplest case, where two environmental states, good and bad, are

randomly distributed and occur with equal frequency:

$$\bar{\lambda}^2 = \lambda_g \lambda_b.$$

Let s measure the departure of good and bad years from the mean. Then,

$$\begin{aligned} \lambda_g &= B(1 + s) + P, \\ \lambda_b &= B(1 - s) + P, \end{aligned}$$

and

$$\bar{\lambda}^2 = \lambda_g \lambda_b = (B + P)^2 - s^2 B^2$$

For the optimum E , $\frac{d\lambda}{dE} = 0$, and

$$\frac{dP}{dE} = -[1 - \{s^2 B/(B + P)\}] \frac{dB}{dE}.$$

Since $0 < [1 - \{s^2 B/(B + P)\}] < 1$ for $s^2 < (P/B + 1)$, optimal effort, E , varies inversely with s (Fig. 6a).

On the other hand, if environmental variability affects adult, rather than juvenile, survival,

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

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

and

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

Thus,

$$\frac{dB}{dE} = -[1 - \{s^2 P/(B + P)\}] \frac{dP}{dE}.$$

Now so long as $0 < [1 - \{s^2 P/(B + P)\}] < 1$, or $s^2 < (B/P + 1)$, increased s favors increased reproductive effort (Fig. 6b).

To summarize Schaffer's argument, a fluctuating environment that has its impact on juvenile mortality favors reduced reproductive effort, smaller clutches, and longer-lived organisms. But environmental variability that affects adult survival favors increased reproductive effort, larger clutches, and short-lived organisms. Table 4 contrasts the bet-hedging predictions with those made by r - and K -selection.

Cody (1971), Gadgil and Solbrig (1972), and Abrahamson and Gadgil (1973) have checked the predictions of r - and K -selection against field data on birds and wildflowers, and they are reasonably well borne out. However, Menge's (1974) work on intertidal starfish shows that other factors can complicate the situation. In starfish living on the open coast, there is a trade-off between reproductive effort and adult mortality, specifically the mortality caused by fluctuations that create the "r-situation." Thus, organisms living in a situation that one would expect to select for an increased reproductive effort actually show a decreased reproductive effort (cf. Williams, 1966b). I know of no published work presenting data that would allow us to discriminate between the alternative explanations listed in Table 4. Such work is badly needed.

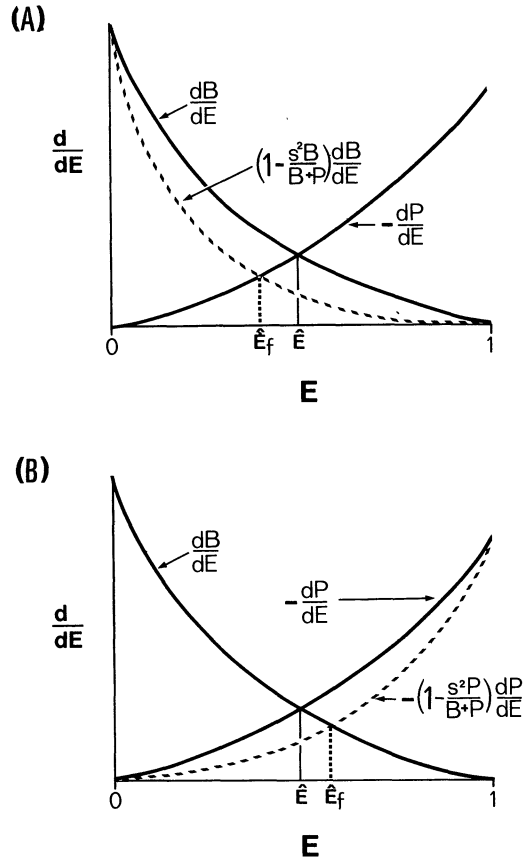


FIG. 6. THE IMPACT OF VARIATIONS IN MORTALITY ON LIFE HISTORIES

(A) Juvenile mortality variable. When variations in mortality affect the number of young that survive to breed, B , then the optimum reproductive effort in a fluctuating environment, \hat{E}_f , is smaller than the optimal effort in a constant environment, \hat{E} .

(B) Adult mortality variable. When the variation in mortality affects parental survival, P , then the optimal reproductive effort in a fluctuating environment, \hat{E}_f , is larger than the optimal reproductive effort in a constant environment. s measures the departure of both good and bad years from the mean. (Adapted from Schaffer, 1974b; see text.)

Life History Tactics In Variable Environments

This section is organized on the basis of a classification of types of variability in physical and biological environments. The criterion used is that of the types of information about the future provided by the histories of different environments (Fig. 7). With each type of environmental variation there are associated some

TABLE 4

The contrasting predictions of r- and K-selection and bet-hedging

(1) r AND K-SELECTION AND BET-HEDGING WITH ADULT MORTALITY VARIABLE	
Stable Environments	Fluctuating Environments
Slow development and late maturity	Rapid development and early maturity
Iteroparity	Semelparity
Smaller reproductive effort	Larger reproductive effort
Fewer young	More young
Long life	Short life
(2) BET-HEDGING WITH JUVENILE MORTALITY VARIABLE	
Early maturity [†]	Late maturity
Iteroparity	Iteroparity
Larger reproductive effort	Smaller reproductive effort
Shorter life	Longer life
More young per brood	Fewer young per brood
Fewer broods	More broods

biological examples and a discussion of whatever theory has been constructed to date. The classification is not logically exhaustive, but neither are the types of variation encountered in nature.

Type 1: Cyclic, Period Fixed and Long (>>T)

Multivoltine temperate insects, temperate cladocerans, pelagic tunicates (Heron, 1972a, b), and a host of other animals inhabit environments in which regular periods of severe stress are punctuated by conditions favorable for colonizing episodes. These circumstances favor low age at first reproduction, large clutch size, and parthenogenesis during the colonizing phase, followed either by (1) sexual mating at the onset of stress to produce a diapause form capable of resisting the stress period (aphids, cladocerans); or (2) developmental plasticity in life-history parameters, producing longer-lived iteroparous forms (pelagic tunicates). The significance of the timing of mating in the former is not known. Some persons think that prediapause sex is adaptive because it increases the genetic variability present in the overwintering clutch of any given parent. Added genetic variability could spread the risk of succumbing to uncertain winter conditions and uncertain

spring hatching times (also see Williams, 1975).

There has been no formal theoretical investigation of optimal life-history tactics in Type 1 environments. However, Levins (1968, Chap. 2) has made a preliminary suggestion that a developmental switch that produces one phenotype above a certain threshold and another phenotype below that threshold will be optimal in such environments (fine-grained in space, coarse-grained in time). The aphids and some open-water cladocerans fit the prediction, but the pelagic tunicates change life-history tactics more nearly as a continuous function of food supply, with no threshold phenomena. Other cladocerans apparently produce ephippia and enter a resting stage long before the seasons change, perhaps to avoid biological rather than climatic stress.

Fleas living on rabbits have available a dependable signal predicting the onset of a colonizing phase: the estrus cycle of their host (Rothschild and Ford, 1972). They have evolved obligate synchronization with their host's breeding cycle. (However, some questions remain open. What happens to fleas living on male rabbits?). Synchronization is only possible because fleas have a capacity for rapid numerical response that enables them to achieve synchrony within the period of the rabbit's breeding cycle.

Type 2: Cyclic, Period Short ($\leq T$)

2a. Cycle predictable

Large organisms living in stable, seasonal environments encounter this situation, e.g., most terrestrial vertebrates and trees—also organisms that either live or spawn in the intertidal zone, e.g., many molluscs, barnacles, starfish, crabs, and the California grunion. Since conditions are predictable, the situation selects breeding at the optimal time, with little variance in breeding time (Cohen, 1971). MacArthur (1968) has pointed out that where the cycle affects age classes differentially, the population will evolve towards a state where its age distribution cycles with the environment, with the most resistant age classes dominating at any time. Certainly part of this synchronization is achieved by selection of breeding time within the cycle, but I know of no examples that

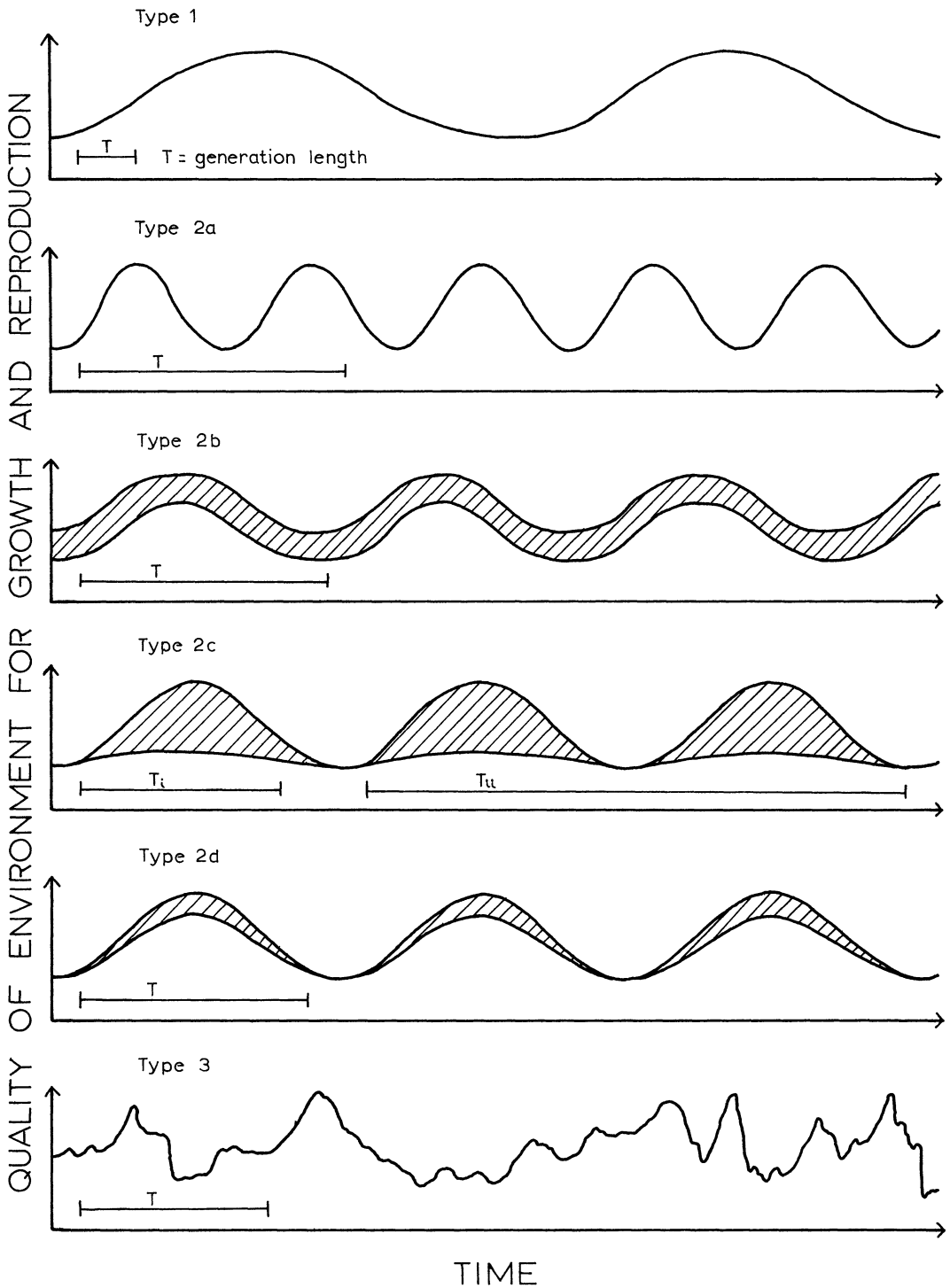


FIG. 7. A CLASSIFICATION OF FLUCTUATING ENVIRONMENTS

By considering the variability and predictability of the environment, relative to the generation time of a population, one finds six general classes. The shaded areas indicate regions of unpredictability in either amplitude or period of fluctuations. See text for explanation.

illustrate the more complex adaptation MacArthur predicted.

For tropical trees that experience a long dry season, Janzen (1967, 1971a, b, 1972a) posited a tactic that channels effort into vegetative growth during the wet season, when competition for light is severe, then into reproduction during the dry season, when pollination and dispersal agents are most dependent on the trees as an energy source. Once the trees are roughly synchronized, coevolved synchrony in the pollinator and disperser populations will make it difficult for trees to reproduce during the wet season, on the one hand, or to decrease the variability in flowering and fruiting time too far on the other. Perfect synchrony will not evolve, because so brief a burst of energy in time would not be worth the attention of specialized, tropical pollinators and dispersers. At the same time, some decrease in variability in fruiting time is advantageous to swamp seed predators (Janzen, 1967, 1971b).

Thus a dynamic balance of community-level forces may determine the onset of the breeding season and the variability of reproductive effort within it, both among and within plant species. The evolution of a predator-swamping effect, following imperfect synchrony owing to optimization of breeding time with respect to physical factors, can also be invoked to explain the mass, synchronous nesting behavior (arribadas) of sea turtles in Costa Rica and the islands of the Indian Ocean (Richards and Hughes, 1972).

Periodic cicadas provide another remarkable example. There are three species, each split into two races, one with a 13-year and the other with a 17-year diapause before emergence. The larvae live in the soil, sucking on tree roots; the entire brood emerges within a period of a few weeks. Lloyd and Dybas (1966) suggested that the long larval phase, combined with large emergence numbers, acts to swamp predators, and that the 13-year and 17-year prime-number life cycles evolved as means of escaping from shorter-lived parasitoids, which would have to achieve diapause periods of similar length before any return would be realized.

2b. Start of cycle unpredictable

This environment is inhabited by some univoltine insects and annual plants. As Cohen (1966) and Boer (1968) have pointed out, the

optimal tactic here is to spread the risk of germinating (or hatching) too soon or too late in the cycle by developing a within-clutch polymorphism in age at first reproduction or in response to environmental cues, or in both. More precisely, the optimal tactic consists of generating a distribution of hatching times in the clutch that matches the historical probability distribution of the optimal date for reproduction. Palmblad (1969) and Marshall and Jain (1970) have found support for this prediction in weedy plants.

2c. Start of cycle predictable, conditions unknown

Period about equal to lifetime. This situation characterizes some univoltine insect and annual plant species towards the limits of their range: on mountain tops, at high latitudes, in deserts (Mayer and Poljakoff-Mayber, 1963), where the probability of a disastrous season in which no reproduction is possible becomes significant. The populations may be maintained by migration from areas with more predictable conditions. Variance in reproductive effort should be high and well correlated with variance in environmental quality.

As pointed out above (p. 000 ff.), environmental conditions that vary from year to year select clutch sizes both smaller and more variable than the most productive size. Some beetles and birds of prey have developed two different methods of generating flexibility for dealing with temporal variability. Owls, hawks, and eagles lay their eggs several days apart, producing clutches in which all the young survive in good years, whereas in bad years the oldest progeny outcompete their siblings for scarce food, and the clutch produces one well-fed fledgling instead of three or four starved weaklings (Burton, 1973). Such flexibility maximizes recruitment in good years while minimizing the risk of total failure in bad years. Carabid beetles of the genus *Agonum*, living in isolated patches of deep leaf-litter in marshes, use a different tactic for generating flexibility, but it has the same result. When poor conditions lower juvenile survival, the beetles decrease their reproductive effort. Since reproduction costs these beetles something in terms of adult mortality, the adults live longer, and normally annual individuals survive into the next season to

reproduce when conditions may be better (Murdoch, 1966).

Period less than lifetime. Larger, longer-lived species, such as tropical trees and birds, experience these conditions. As Cohen (1966) and Boer (1968) have emphasized, under these conditions it pays to produce a clutch smaller than the most productive (see Fig. 3). It also pays to increase the variance in breeding time among the progeny. Nidicolous birds living in temperate areas should decrease clutch size as the season progresses in order to put more effort into each chick and to fledge the clutch in time for winter. About sixty bird species show a decline in clutch size from the start of the season (Klomp, 1970), but whether the decline is adaptive is not known. Several authors have suggested that the decline is not adaptive and is produced by the smaller effort made by late breeders, who have usually already failed at one clutch, or are breeding for the first time (Klomp, 1970). Holgate (1967) and Murphy (1968) have pointed out that in such circumstances iteroparity and longer lifetimes are favored because they reduce the risk of the animals getting completely eliminated in one bad year.

In focusing on dormancy tactics, Cohen, (1967) postulated that the long-term population growth rate reflects the balance between the proportion of progeny germinating in any given year, and the proportion dying during dormancy over the next year if they do not germinate. In other words, spreading the risk is advantageous, but how far the risk gets spread is determined by a balance between the seriousness of the risk and the cost of spreading it. More precisely, a mixed tactic, where only a fraction of the population reproduces, results when the variabilities of the outcomes of reproducing and of not reproducing increase relative to the difference between their means (Cohen, 1968). In a further analysis of the distribution of reproductive versus vegetative (somatic) growth in an unpredictable environment, Cohen (1971) found that when conditions are uncertain, the optimal tactic is to spread out the production of seeds and leaves. This pattern is found in some desert annual plants.

Mountford (1971) also emphasized the importance to individuals of retaining a certain proportion of progeny with delayed reproduc-

tion in order to minimize the risk of extinction. The power of this selection factor will increase as population sizes decrease. In particular, the proportion of progeny developing each season reflects a balance between minimizing the probability of extinction and maximizing the long-term growth rate. The wild oats *Avena fatua* and *A. barbata* may provide one example (Marshall and Jain, 1968, 1970).

2d. Start predictable, conditions partially known

Large, long-lived vertebrates, some trees, and some parasites and commensals inhabit this environment. One tactic is to skip reproduction completely if conditions indicate a bad season ahead; and even, if reproduction is mistakenly attempted, to resorb the embryo or carry it over in a resting state until better conditions prevail, as, e.g., in the case of the red kangaroo in the Australian desert (Short, 1972) or fleas living on rabbits (Rothschild and Ford, 1972).

Cohen (1967) has analyzed diapause strategies in this context. He predicted that the organisms will lock in on environmental variables that are correlated with future conditions, and will produce a probability distribution of diapause times in their progeny that reflects the probability distribution of breeding times predicted by the environmental cues. However, the interests of parents and progeny may conflict, for each of the offspring should time its emergence from diapause to hit the peak of the breeding season, rather than arrive either early or late as the result of parental optimization (cf. Trivers, 1974).

Many temperate conifers are known to have mast years (years of heavy seed production) alternating with years in which there is little or no seed production (seed crop "failure"). Mast years are common in the Douglas Fir (*Pseudotsuga menziesii*) in British Columbia (Smith, 1970), and reach their most extreme development in the monotypic stands of *Pinus cembra* in the Russian taiga, where there are 8- to 11-year periods between seed crops (Janzen, 1971a). At least three factors influence masting. (1) It may take a number of years of vegetative growth to build up the energy needed to reproduce with any chance of success for a wind-pollinated species that must produce a large pollen crop. (2) Environmental signals

available at the start of a breeding season may occasionally indicate favorable conditions ahead. The pine trees would respond to such signals with a strong, but incompletely synchronous, response. (3) This imperfect synchrony in mast years will be reinforced by predators which eliminate seed crops set in off years, but are swamped by the amount of seed produced in mast years (Smith, 1970; Janzen, 1971a).

The annual fishes studied by Wourms (1972) provide a much better and more thoroughly analyzed example. He said:

Annual fishes can maintain permanent populations in temporary aquatic habitats since the population survives dry seasons in the form of diapausing eggs. Populations persist even though subject to erratic environmental cycles and recurrent ecological catastrophes. . . .

Survival strategy is based on the "multiplier effect"; i.e., interposition into the developmental pathway of *three* branch points containing diapause stages of prolonged, variable duration generates *eight* different distributions of total developmental time. Thus, a single egg population of identical age can generate several subpopulations, all of which develop according to different schedules. A developmental program is established which permits the repeated loss of individual eggs under conditions which may initiate hatching but do not allow for maturation and successful reproduction. The "multiplier effect" augmented by other adaptations guarantees that some portion of the egg population will survive to reproduce (Wourms, 1972: p. 389).

Wourms's exemplary studies establish clear links between the details of the developmental biology of a species and the ecological problems posed by the situation in which it evolved. We need much more work like his, but two types of information would make his story more complete. First, the genetics underlying the distribution of diapause types should be elucidated; and secondly, the relationship between the frequency of diapause types in local populations and the distribution patterns of rainfall should be established on a comparative basis over a geographical range broad enough to provide a diverse sample of types of climatic variability.

Type 3: Random In Time

No theoretical work on optimal life-history tactics has been done for this type of environ-

ment. The conditions during the habitable period may be either predictably favorable, predictably unfavorable, or unpredictable. Microorganisms inhabiting ephemeral environments are one type of organism encountering these conditions, e.g. terrestrial rotifers, paramecia, unicellular algae, and other species dependent on rainfall for the opportunity to grow and reproduce. Inhabitants of temporary ponds provide another example. When conditions are favorable, the optimal tactic should be rapid development and a total commitment of available energy to reproduction that produces a resting stage. When conditions are unpredictable, a mixed tactic of producing some progeny that hatch at the first encounter with growing conditions, others at later encounters, is favored, e.g., by fairy shrimp.

Plants dependent on fire for seed release and germination meet these conditions on a larger time scale. Tactics can take at least two forms: holding the seeds on the tree until a fire passes through, e.g., lodgepole pine, *Pinus contorta*, on the eastern slope of the Rockies (Smith, 1970); or releasing seeds into the soil but making germination dependent on heat shock, e.g., many prairie grasses. In both examples, reproductive effort is stored in potential form (seeds) when conditions are favorable for growth, and development depends on a signal from the randomly distributed environmental variable.

Timing The Amount And Distribution Of Effort

The previous section has emphasized the problems of optimizing the pattern in time of reproduction and diapause in the face of various temporal patterns of environmental fluctuation. This section deals with the same problem in homogeneous environments. The question was first posed by Fisher (1930) in one of the most frequently quoted passages of his often-quoted book (Williams, 1966b; Taylor, Gourley, Lawrence, and Kaplan, 1974):

It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction (p. 47).

I have built this section on a foundation provided primarily by Williams (1966a, b). In his book, *Adaptation and Natural Selection*, Williams differentiated between the total effort the adult puts into its progeny, on the one hand, and the partitioning of that effort into a few large young or many small young. Svardson (1949) made the same distinction, and anticipated many of Williams's ideas, while Lack (1954) mentioned the trade-off between size and number of young in discussing clutch size. I will first review the ideas and evidence relevant to the partitioning problem, then cover the question of dividing resources between somatic growth and reproduction.

A Few Large vs. Many Small Young

Let us assume that the eggs should be laid at a size which yields the maximum growth rate on the parental investment. The effective growth is the average growth rate of individuals towards reproductive maturity minus the loss to mortality. In a population that is not growing rapidly, the number of offspring decreases over time owing to mortality, and unless the growth rate of the surviving offspring more than makes up for the loss, the net yield on reproductive effort will be negative. If progeny can grow faster as larvae outside the parent (when resources for the young are abundant, and predation pressure is low), then many small progeny will be favored. If resources for young are scarce, or predator risk to small size classes is high, then the parent will tend to produce a few large progeny. In such circumstances, live-bearing will be favored over egg-laying if internal fertilization is possible, because live young do not experience the start-up time of eggs that have to develop before they can begin assimilating energy and grow, and because live young generally experience lower mortality rates than eggs do. (This is an abstract of an argument given by Williams, 1966a, Chap. 6).

In the light of this argument, Williams was puzzled by the low incidence of viviparity in insects, and its absence from birds. However, Neill suggests (pers. commun.) that viviparity will not be advantageous to insects that overwinter as eggs, nor to birds, which must minimize weight in order to fly properly. (Most birds will carry one heavy egg in flight, but I know of no bird that carries a full clutch. The eggs

mature one at a time.) Furthermore, Neill notes that most temperate insects encounter few predators and ample food when they first hatch in the spring, and thus violate the assumptions Williams made in deducing his prediction of viviparity.

Gotto (1962) reviewed egg size and egg number in commensal and parasitic copepods, and suggested the following story. Where the host is abundant, readily accessible, and easy to find, and where environmental conditions are stable (calm, sheltered waters), then a few large eggs will be favored, because larger eggs produce larger larvae, which have a competitive advantage in the scramble for the few available sites in a saturated environment. On the other hand, where the host is sparsely distributed, inaccessible, hard to find, or highly mobile, or where the host's habitat is unstable or difficult to penetrate (the intertidal, wave-beaten shores), then many small eggs will be favored, because they can sample more of the environment and reduce the risk that the clutch will fail to produce any mature progeny.

Gotto's review of the data supports this picture on the whole, although several poorly understood species break the main trends. Gadgil and Solbrig (1972) would call the group producing a few large eggs *K*-selected, and those producing many small eggs *r*-selected. They have suggested that a similar situation obtains in wildflowers. Price (1973) noted similar trends in ichneumonid wasps, a family parasitic on insect hosts. Different wasp species lay their eggs in different stages of their host's development. Those laying on early instars have many small eggs; those laying on later instars have a few large eggs. Price suggests that this trend can be explained in terms of adjusting the fecundity to the probability of survival. To explain the trend, one could also invoke the ideas of Williams and Svardson on the competitive advantages of a few, large young. There is a correlation in mammals between increased parental care and fewer, larger progeny. Williams (1959) showed, that this correlation did not exist in the darters, where only the males care for the young, and was at least clouded in other fish by the confounding correlation of egg numbers with body size, which is not necessarily related to parental care.

Janzen (1969, 1971b, 1972b) and Harper, Lovell, and Moore (1970) have reviewed the

problem of what determines seed size and seed number in plants. Most plants, especially in the tropics, exist in a complex coevolutionary context, contending with seed and seedling predators (chiefly fungi, viruses, insects, mammals, and birds), and benefiting from dispersal agents (wind, water, insects, birds, and mammals). Optimizing seed design for one purpose does not necessarily optimize it for another: an intermediate compromise must be reached. (Some plants produce a mixture of large and small seeds, but even here decisions must be made on dividing resources between the large and the small seeds—cf. Harper, Lovell, and Moore, 1970). For example, many small seeds are favored both for wind-dispersal and for avoiding attack by beetles that lay their eggs in the seeds. If a seed can be made small enough, it may be too small for a larval beetle to develop in it. But large seeds with thick, hard coats can escape many seed predators, and have the energy reserves to send up a large, competitively superior seedling. Many plants produce seeds impregnated with noxious chemicals, presumably at some cost. There is considerable evidence that this also reduces seed predation (Janzen, 1971b).

There are difficulties intrinsic to the give-and-take of coevolutionary interactions that make detailed predictions difficult and the sorting out of the post hoc, plausible explanations commonly found in the literature well-nigh impossible. A great deal depends on the exact nature of the species and the community involved. Switching from one size of seed to another to escape a size-selective predator may be no advantage if there is another predator in the community ready to switch onto your seeds as they change in size.

Many plants and some animals (e.g., *Hydra* and other coelenterates) can reproduce vegetatively. As Williams (1975) points out, sexual reproduction can have several advantages over asexual reproduction. It always generates variability through genetic recombination, and usually has evolved to permit dispersal and create a propagule that can be made resistant to harsh circumstances. Vegetative, or clonal, reproduction, on the other hand, preserves successful genotypes, placing progeny in an environment that has been tested and found to be favorable—assuming, of course, that conditions do not change. Given that option,

how much effort should the individual put into vegetative as against sexual reproduction at different ages and under different conditions? And why is sexual reproduction associated with dispersal and with resistant propagules? There is a growing literature that focuses on these questions, and since the problems of sexual versus asexual reproduction are complex enough to place them beyond the scope of this paper, I refer the interested reader to Maynard Smith (1971), Williams and Mitton (1973), and Williams (1975).

Sarukhan (1974) and Sarukhan and Harper (1973) studied the population dynamics of three species of buttercups. Two species could reproduce vegetatively. Almost all recruitment to the population on the part of one, *Ranunculus repens*, was owing to vegetative reproduction, whereas, of the other two species, one reproduced strictly sexually (*R. bulbosus*), and one *R. acris*, by a mixture of the two means. Vegetative reproduction proved much more dependable than seed production as a means of persisting locally. The species that put most of its effort into vegetative reproduction, *R. repens*, also produced a small seed crop that had a long dormancy period in the soil. The two sexually reproducing species produced large seed crops, practically all of which germinated in the next year. It seems likely that the allocation of effort between vegetative and sexual reproduction will be strongly influenced by the probability of local extinction, competition, and the problems associated with dispersal and germination. More exemplary studies like Sarukhan's are needed to enable one to assess the factors affecting this decision.

Timing The Amount of Reproductive Effort

Williams (1966a, b) was the first to formulate clearly the problem facing a species or population of deciding how much of current resources to commit to reproduction now, inasmuch as a commitment of resources to the present carries with it some cost to the future. His rule for optimizing current effort is to increase current commitment so long as the current profits more than outweigh the future losses caused thereby. Table 2 presents evidence that in the few cases studied, a greater reproductive effort does increase mortality. Thus, according to Williams, since reproductive value decreases

beyond a certain point with age, reproductive effort should always increase with age. Gadgil and Bossert (1970) derived the same conclusion from their simulation model, but Fagen (1972) constructed a model animal for the Gadgil-Bossert simulation for which reproductive effort first decreased, then increased with age. As Schaffer (1974a) has rightly pointed out, this example reveals the weakness of simulation studies. The results are only as general as the examples used, and it is hard to be sure that you have explored the parameter space thoroughly enough to talk about general conclusions.

If clutch size is taken as proportional to reproductive effort, we find that field evidence regarding clutch size in birds shows that reproductive effort does increase with age, with the exception of the partridge in England (Klomp, 1970). Or if we take the ratio of ovary weight to the $2/3$ root of body weight (to correct for changes in the ratio of digestive surface area to body mass) as being proportional to reproductive effort, we then find that reproductive effort increases with age in several fish, *Hippoglossoides platessoides*, *Melanogrammus aeglefinus*, *Clupea harengus*, and *Clupea pallaseii* (Gerking, 1959; Iles, 1974). These definitions of reproductive effort are inadequate because reproductive effort should properly be considered a rate phenomenon: the rate at which resources in excess of maintenance requirements are diverted into reproduction rather than growth. In the absence of better measures, they do serve to indicate the gross outlines of trends that, it may be hoped, will be more fully and more rigorously investigated.

Theory

Gadgil and Bossert (1970), Schaffer (1972, 1974a), and Taylor et al. (1974) have looked at different aspects of reproductive effort, all of them starting from a focus provided by the work of Fisher and of Williams.

Growth and reproductive effort. Gadgil and Bossert (1970) defined reproductive potential, B , at a given size, w , as the number of offspring produced by an organism of size w that makes the maximum possible reproductive effort. They defined the maximum potential contribution to fitness at a given size, $F'(w)$, as the number of offspring produced by an organism

that makes the maximum possible reproductive effort at the earliest age at which that size is reached. Since reproductive value declines with age in a growing population, $F'(w)$ will be lower than $B(w)$ at greater sizes. If reproductive potential increases slowly with size, then the size of maximal contribution to fitness can be much lower than the size of greatest reproductive potential.

For a big-bang reproducer, reproduction should occur at the age and size corresponding to the peak in the $F'(w)$ versus w curve. For repeat-reproducers, growth should continue as long as reproductive potential increases with size, stopping when reproductive potential has reached a maximum. Sexual maturity will not be postponed beyond the peak in the $F'(w)$ versus w curve, but may occur earlier, especially if the slope of the curve is gentle. When this happens, growth will continue beyond maturity, and reproductive effort will increase rapidly with age. Gadgil and Bossert predict that perennial plants and fish that show this pattern should have a gradual rise in the $F'(w)$ versus w curve. But where the contribution to fitness at a given size, $F'(w)$, increases rapidly with size, growth should cease at maturity, reproductive effort should be high from the very beginning, and reproductive effort should increase only slowly with age. Gadgil and Bossert predict that birds and mammals that show this pattern should have a sharp rise in the $F'(w)$ versus w curve.

The delayed effects of reproduction. Schaffer (1972, 1974a) looked in detail at the interaction of a reproductive commitment at one age with the optimal tactics for subsequent age classes. First, in a simple model where he assumed that survival rates do not change with age and that fertility grows geometrically, Schaffer derived

$$\lambda(E) = b(E) + p(E)g(E)$$

from Lotka's equation, where $b(E)$ is the birth-rate of individuals in the first age class, $p(E)$ is the survival rate, and $g(E)$ is the rate at which fertility grows with age. Clearly, the optimal effort will depend on the shape of the $b(E)$ and $p(E)g(E)$ versus E curves. Schaffer analyzed these curves graphically, and concluded:

- (1) If both $b(E)$ and $p(E)g(E)$ are *convex*, the optimal effort is all-or-none; the animals either commit suicide in reproducing, or skip a year.
- (2) If both $b(E)$ and $p(E)g(E)$ are *concave*, the

optimal effort is intermediate (regular iteroparity).

- (3) If $b(E)$ is an increasing sigmoid, and $p(E)g(E)$ is a decreasing sigmoid, the optimal effort varies according to the initial conditions; the animals either make a total commitment (big-bang suicide), or put forth an intermediate level of effort (iteroparity).

In a more complex model incorporating age structure, Schaffer showed that optimizing the reproductive effort is equivalent to optimizing

$$b_i + p_i g_i V(i + 1)$$

where b_i is the number of female progeny born to a female of age i , p_i is the probability of surviving from age i to age $i + 1$, g_i represents the factor by which fecundity at age $i + 1$ exceeds fecundity at age i , and $V(i)$ is reproductive value at age i .

That is, the optimal life history maximizes, at every age, the sum of present births and future expected births. In essence, the evolutionary rule in both models is always to optimize the current reproductive value based on expected returns from current reproductive effort: young born this season plus expected returns from young born in future seasons, discounted back to the present, and weighted by the probability that the parent will survive to give birth to them. This result was anticipated by Williams (1966b), Hamilton (1966), and Emlen (1970), all of whom stated it indirectly or implicitly. Schaffer was the first to state it directly and to begin an analysis of its consequences.

To see how this conclusion follows logically from demographic assumptions, consider the following reasoning. Using Lotka's characteristic equation,

$$1 = \sum_0^{\infty} b_i l_i e^{-rn}$$

we isolate a single age group, j ,

$$1 = \sum_0^{j-1} b_i l_i e^{-rn} + l_{j-1} p_j e^{-rj} (b_j + p_j V_{j+1}).$$

Now consider the effects of varying births at the given age, j ; that is, we ask the question, "How rapidly does future worth change, and in what direction, as a result of changing current reproductive commitment?" All terms that do not contain b_j or p_j are constant, so

$$1 = A + B(b_j + p_j V_{j+1})$$

and

$$b_j = C - p_j V_{j+1},$$

where A , B , and C are defined by the last two equations. Thus, as Goodman (1971) showed for the comparable continuous case,

$$\frac{\delta b_j}{\delta p_j} = -V_{j+1}.$$

This differential equation defines the locus of points (b_j, p_j) such that r , the population growth rate, is constant. Now consider trade-offs between births, b , and survival to the next breeding season, p , as graphed in Fig. 8. The straight lines represent the family of solutions to

$$\frac{\delta b_j}{\delta p_j} = -V_{j+1}.$$

r increases as the lines march out to the right. Thus r is maximized when the trade-off curve of births versus survival intersects with that member of the family of straight lines

$$b_j = C - p_j V_{j+1}$$

that is farthest to the right. (I am grateful to Ric Charnov for showing me this derivation).

Schaffer went on to analyze graphically the coevolution of age-specific efforts in a three-stage life history. Certain shapes of the relationship between effort at one age and reproductive effort at the next generate two stable equilibria, one predicting semelparity, the other iteroparity. Which one evolves will depend on the initial conditions, i.e., the reproductive tactics of the ancestor. Schaffer suggests that this may explain why iteroparous steelhead exist side-by-side with semelparous salmon (cf. Fig. 9). An alternative explanation is that semelparity had to be adaptive to be evolved, but need not have been adaptive to be retained. "Once all of the life cycle that follows the first reproduction has completely atrophied there would be no way of re-establishing it. The change from iteroparity to semelparity should be irreversible" (Williams, pers. commun.). Both explanations are good examples of the plausible, but not testable, interspecific comparisons discussed in the introduction.

An analytic approach. Taylor et al. (1974) have established several potentially useful theorems concerning populations in a stable age distribution. Dealing with Lotka's characteristic equation as a definition of r , and with

Fisher's definition of reproductive value, they proved that:

1. Maximizing the reproductive value at age zero is mathematically equivalent to maximizing the ultimate rate of increase (p. 109).
2. . . . in order to maximize the reproductive value at age zero, the reproductive value must be maximized at every age, taking into account the organism's development up to that time. This principle of successive life history optimization must result in the fittest strategy (p. 111).

In applying their results to life-history patterns that incorporate the effects of growth and the costs of reproduction, they established, as did Schaffer (1974a), that if the number of offspring is a convex or linear function of reproductive effort, then the organism will either grow or reproduce, but not both, i.e., it will adopt a big-bang tactic. Taylor et al. also established that if the energy available for growth and reproduction is a concave function of biomass, and the mortality rate is constant, then selection favors determinate growth. This second result refines Gadgil and Bossert's assertion that determinate growth is a result of a life-history pattern showing a rapid rise in reproductive potential with size.

Evidence

Williams (1966a, b) has suggested the following correlates of increased reproductive effort: a larger ratio of progeny weight to female body weight, more clutches per season, brighter coloration in breeding males, more lengthy and elaborate courtship displays, more territorial and aggressive behavior, viviparity rather than oviparity, and more parental care. Tinkle (1969) demonstrated trends in all these parameters that showed, in general, that early-maturing lizard species were showing the other signs of increased reproductive effort that one would expect from Williams's predictions.

Tinkle, Wilbur, and Tilley (1970) found that early-maturing lizards also tend to have several small clutches per season and larger per-season fecundities than do the late-maturing lizards, which produce a single, large clutch. These general trends are matched in birds (Cody, 1971), whose life-history tactics can be separated into two groups: (1) those having early maturity, large clutches, and short reproductive spans, e.g. passerines, and (2) those having late ma-

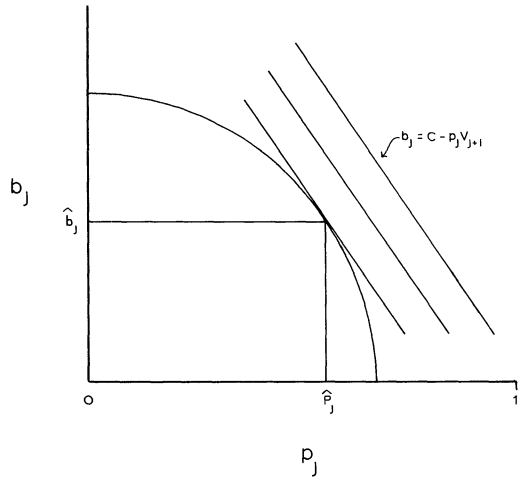


FIG. 8. A GRAPHICAL ARGUMENT ON OPTIMIZING REPRODUCTIVE EFFORT

Consider a life history in which we isolate a single age class, j , and allow births and adult survival to vary for that age class alone while holding the rest of the life history constant. Then that combination of reproductive effort, as reflected in births (b_j), and adult survival to the next breeding age (p_j), is optimal which maximizes $b_j + V_{j+1}$. That point can be determined graphically, as shown in the figure, but the actual values, and whether or not there are one or more combinations of b_j and p_j , will be determined by the shape of the curve.

turity, small clutches, and long reproductive spans, e.g., raptors and large seabirds. Also, for wildflowers, Gadgil and Solbrig (1972) demonstrated that plants growing in disturbed sites devoted greater effort to reproduction than did plants growing in undisturbed sites. By making appropriate assumptions about environmental conditions and the shape of the curves relating reproductive effort and adult survival, one can explain all these observations as optimization of current reproductive effort plus expected future returns. In none of the above cases, however, was the shape of the trade-off curve measured.

Schaffer and Tamarin (1973) showed that population cycles in voles could be explained as resulting from the lagging of changes in the optimal point for reproductive effort slightly behind density changes, the proximate cause being an increase in juvenile mortality as density increased. In essence, they showed that their model could account for the observed fluctua-

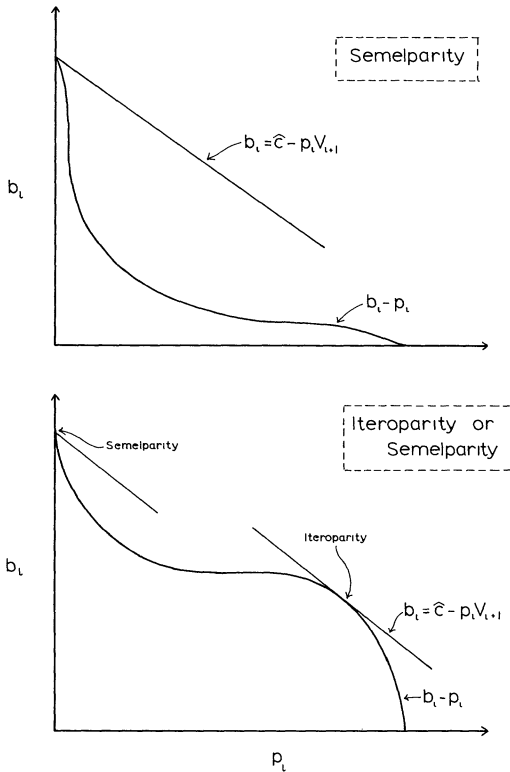


FIG. 9. A GRAPHICAL ARGUMENT ON REPRODUCING ONCE OR MANY TIMES

Schaffer's (1974a) trade-off model predicts that under certain assumptions about the shape of the trade-off curve between reproductive effort and adult survival, either semelparity or iteroparity may evolve depending on initial conditions. The upper example shows conditions under which only semelparity will evolve; the lower, either. b_t , progeny born at age i that survive to reproduce; p_t , probability that the parent will survive to breed again; $b_t - p_t$, trade-off curve of births vs. adult survival. See text for derivation of $b_t = C - p_t V_{t+1}$.

tions, but that it was not mutually exclusive of others proposed. Furthermore, Schaffer and Elson (1975) showed that much of the variability in age at first reproduction in Atlantic salmon could be explained in terms of a trade-off between the cost of (1) reproductive effort as measured by the length of the river, and (2) future returns as measured by the growth rate at sea.

Summary

The theories arising from Williams's conjecture have proved to be provocative and have

been well enough confirmed to be worth pursuing. Now we need measurements of the actual trade-offs between adult survival and reproductive effort to generate the shapes of the curves necessary to test the graphical arguments put forth by Gadgil and Bossert (1970) and by Schaffer (1974a). Until someone actually measures the shapes of the curves in the field, we will be left with unsatisfactory, post hoc explanations.

DISCUSSION

This review has dealt with a large volume of material, and a discussion could take many directions. I shall restrict my comments to three areas. First, I will criticize a recent trend in the life-history literature. Second, I will examine what conclusions we can draw from the review about the general evolutionary causes of observed trends in life-history phenomena. Third, I will ask what implications the review has for the design of theoretical and experimental research projects.

Scholasticism or Empiricism?

Since the approach taken in several of the papers I have reviewed (e.g., Cody, 1966; MacArthur, 1968; Gadgil and Bossert, 1970; Mountford, 1971, 1973) represents an unfortunate trend in ecological studies, I am going to criticize them quite severely. In so doing, I criticize the trend as much as the ideas in the particular papers that exemplify it. For example, Gadgil and Bossert presented a number of ideas (e.g., that of F') that, while charming and plausible, generate predictions that are absolutely unfalsifiable. Therefore, they do not constitute science as I understand it. Recently, many papers have appeared which disregard a consideration of hard evidence in preference for a discussion of ideas for their own sake.

To an alarming degree, the attitude that sanctions such speculations in a vacuum of evidence spurs two additional objectionable trends. First, theories accumulate, few of them formulated in common terms, much faster than evidence can be assembled to test them. The result is a confusion of untested ideas which are judged, not on their ability to withstand empirical tests, but on the difficulty of the mathematics used or the obscurity of the theo-

retical development. Clearly, such criteria are inappropriate. Second, that such papers are accepted and published spurs a casual disregard for the hard work involved in rigorous empirical tests. Not only do theories accumulate, but the manner of their accumulation decreases the likelihood that they will be tested. An enormous amount of effort is being put into the development of ideas for which no one has established connections with the real world. If the field is to progress, we must get away from the practically Scholastic approach surfacing in such papers, and get back to rigorous empiricism.

Theoretical work should be carefully done and clearly communicated, and should result in predictions that are at least potentially falsifiable. In all cases, alternative explanations should be impartially considered in the light of the best available evidence. That papers that do not meet these criteria are getting past referees and editors disturbs me, for it may mean that the nature of science is broadly misunderstood. Our purpose is not to have beautiful ideas, or profoundly obscure ideas, but to arrive at explanations that meet the most rigorous challenges that evidence and logic can pose.

Patterns Of Causation

Tables 5 and 6 present an abstract of the hypotheses reviewed above. Two patterns stand out from the tables. First, for any given trend in life-history traits, e.g., an increase in clutch size, there are several plausible hypotheses, not mutually exclusive, that could explain the trend, either singly or in combination. Second, although there is no standard method for approaching the evolution of life histories, different authors repeatedly emphasize the same points. The important life-history traits are both the mean *and* the variance in age at first reproduction, clutch size, size of young, number of clutches per lifetime, and inter-brood interval. A given combination of these traits is a life-history tactic. The evolution of life-history tactics is strongly influenced by the pattern of variation in space and time of relevant environmental variables. Among the multitude of environmental factors, those most generally relevant to life histories are food, temperature, breeding sites, refugia, competitors, and predators. However, in specific cases other factors may dominate.

The standard organism-environment dichotomy used in the previous paragraph dangerously oversimplifies the situation. To the population, the definition of the "environment" depends on the biological characteristics that the population has already evolved. As one characteristic changes under selection pressure, e.g., age at first reproduction and with it generation time, the definition of the "environment" changes, perhaps from irrelevant noise to significant fluctuation, or from being unpredictable to being effectively constant. Such changes in the definition of the environment will affect profoundly the further evolution of other traits. For any individual trait, the definition of the "environment" includes the current states of all other traits in the population. Traits co-evolve. As one trait changes under selection pressure from a classic external environmental variable, such as an increase in population density, other traits will undergo compensatory or opportunistic changes owing to the redefinition of their relative "environments." The work of Lewontin (1965) and Meats (1971) has provided an indication of where this line of thought could lead.

Thus, two factors complicate the simple cause-effect relationship in terms of which we usually think. In general, several evolutionary causes, possibly operating at the same time, can produce the same effect in a population's life history. Furthermore, a given external environmental factor may well affect a number of traits that will, as they change, redefine the "environment" and thus the "optimum tactic."

Within the biological community, there is a subterranean split between those who believe that for every phenomenon there is a single cause at a given level of explanation, and those who believe that there can be multiple causes for certain phenomena operating at the same level of explanation. Because this split is rarely articulated, it can block intelligent discussion. Furthermore, people who prefer to deal with ideas one at a time may not recognize the potential importance of multiple causes. The problem is serious; it erects mental blinders that lead researchers to argue with the misleading consequences of unarticulated presuppositions, rather than deal directly with the presuppositions themselves, with the logical difficulties of certain theories, or with the admissibility of given evidence. Although this problem is certainly not unique to life-history theory,

TABLE 5
A summary of the causal systems hypothesized to affect the evolution of life-history patterns

(1) THE EVOLUTION OF THE NUMBER OF CLUTCHES IN A LIFETIME—SEMELIPARITY VS. ITEROPARITY		Trend: Decrease in the Number of Clutches		Reference	
CAUSAL SYSTEM					
a.	Increase in adult survival relative to juvenile survival	a.	Increase in juvenile survival relative to adult survival	Harper, 1967	
b.	Increased probability of total reproductive failure in any particular season: unstable, unpredictable environments	b.	Decreased probability of total reproductive failure in any particular season: stable, predictable environments	Holgate, 1967; Charnov & Schaffer, 1973	
c.	K-selection: constant environments, more clutches resulting from longer life	c.	r-selection; variable environments, fewer clutches resulting from shorter life	Pianka, 1970	
d.	Increased need for parental care	d.	Decreased need for parental care		
(2) THE EVOLUTION OF CLUTCH SIZE					
Trend: Increased Number of Progeny of a Constant Size		Trend: Decreased Number of Progeny of a Constant Size		Reference	
a.	Increased food availability leading to an increase in total resources available for reproduction	a.	Decreased food availability leading to a decrease in total resources available for reproduction	Lack, 1954	
b.	Decrease in the resources required for competition, predator avoidance, maintenance, and migration	b.	An increase in the resources required for competition, predator avoidance, maintenance, and migration	Skutch, 1949, 1967; Cody, 1966	
CAUSAL SYSTEM					
c.	r-selection: —increased density-independent mortality relative to density-dependent mortality —more variable or unpredictable climate —decrease in adult survival; decrease in competition	c.	K-selection: —increased density-dependent mortality relative to density-independent mortality —more stable climate —increase in competition	MacArthur & Wilson, 1967 Murphy, 1968 Pianka, 1970	
d.	Decrease in the slope of a linear trade-off between adult mortality and reproductive effort or increased concavity of a nonlinear trade-off	d.	Increase in the slope of a linear trade-off between adult mortality and reproductive effort or increased convexity of a nonlinear trade-off	Charnov & Krebs, 1973, (my interpretation of their graph)	

e. Increase in predictability of conditions during the breeding season, at the start of the season (for iteroparous organisms)	e. Decrease in predictability of conditions during the breeding season, at the start of the season (for iteroparous organisms)	Charnov's interpretation of Cohen, 1967 and Boer, 1968
(3) THE EVOLUTION OF THE PARTITIONING OF REPRODUCTIVE EFFORT INTO PROGENY OF VARIOUS SIZES		
Trend: Fewer, Larger Progeny		
Trend: More, Smaller Progeny		
CAUSAL SYSTEM		
a. Food for young scarce	a. Food for young plentiful	Williams, 1966
b. Size-selective predation on small young	b. Less size-selective predation on young	Williams, 1966
c. Habitat plentiful, easily accessible, and saturated	c. Habitat scarce, hard to find, and unsaturated	Gotto, 1962
d. Environmental conditions stable	d. Environmental conditions variable and/or unpredictable	Gotto, 1962
e. K-selection	e. r-selection	Gadgil & Solbrig, 1972
f. Increased competitive demands on young	f. Decreased competitive demands on young	Janzen, 1969;
g. Predator-swamping irrelevant	g. Predator-swamping important	Harper, 1970
Trend: Earlier Reproduction		
Trend: Delayed Reproduction		
(4) THE EVOLUTION OF AGE AT FIRST REPRODUCTION		
Trend: Earlier Reproduction		
Trend: Delayed Reproduction		
CAUSAL SYSTEM		
a. Population expanding	a. Population stable at saturation level	Cole, 1954;
b. Accumulated reproductive value, conditional on not reproducing and averaged over age, starting to decline with age	a. Population declining	Lewontin, 1965
c. Decrease in cost of reproduction in terms of adult mortality	b. Accumulated reproductive value, conditional on not reproducing and averaged over age, still increasing with age	Hamilton, 1966
d. Decrease in growth in intervals between breeding (for iteroparous organisms)	c. Increase in cost of reproduction in terms of adult mortality	Mertz, 1971a, b
	c'. Entry to breeding population restricted by a hierarchical social system	Gadgil & Bossert, 1970
	d. Increase in growth in intervals between breeding (for iteroparous organisms)	Schaffer, 1972
		Schaffer & Elson, 1975
		Geist, 1971
		Schaffer & Elson 1975

TABLE 6
Evolution in fluctuating environments: a taxonomy of tactics

ENVIRONMENTAL SITUATION	TRAITS SELECTED	EXAMPLES	REFERENCES
I. Cyclic, fixed period, period >> lifespan	<ol style="list-style-type: none"> 1. Reproduction early in cycle 2. Large clutches 3. Parthenogenesis 4. Diapause forms 	Aphids, cladocerans, pelagic tunicates, multivoltine insects	
II. Cyclic, period fixed, period < lifespan:			
a. Start of cycle and conditions during cycle predictably favorable	<ol style="list-style-type: none"> 1. Synchronization of breeding time at optimal point in cycle 2. Synchronization of release of young to swamp predators 3. Separation of vegetative (somatic) and reproductive effort in time 	Many ungulates many trees, intertidal organisms periodic cicadas, sea turtles	Janzen, 1971b
b. Start of cycle predictable only within limits, cycle predictably favorable	Spread risk by developing within clutch variance in hatching on germination date to match the historical probability distribution of the optimum	Univoltine insects, annual plants near center of their range	Cohen, 1966; Palmblad, 1969; Marshall & Jain, 1970
c. Start of cycle predictable but conditions during cycle unpredictable; no information on future conditions available at start of cycle	<ol style="list-style-type: none"> 1. Iteroparity and long lifespan 2. Larger variance in diapause length 3. Intermingling of vegetative and reproductive growth during the season; several clutches per season 	Univoltine insects and annual plants near limits of their range; desert plants, wild oats, annual fish	Cohen, 1968, 1971; Mountford, 1971; Marshall & Jain, 1968, 1970; Wourms, 1972
d. Start of cycle predictable, conditions during the cycle unpredictable but some information available on the future	<ol style="list-style-type: none"> 1. Ability to resorb reproductive tissue 2. Flexible timing of reproduction 3. Ability to skip a season entirely if it looks bad, e.g., mast years 	Condors, albatrosses, the red kangaroo, trees	Short, 1972; Smith, 1970; Janzen, 1971b
III. Not cyclic, but distributed as a random variable in time	<ol style="list-style-type: none"> 1. Rapid development, large reproductive commitment 2. Ability to resorb reproductive tissue if a mistake has been made 3. Ability to enter a resting stage as an adult 	Microorganisms?	

nowhere does it cause more problems.

For example, we should remain open to the possibility that the assemblages of traits, the tactics, predicted by r - and K -selection or by bet-hedging, or their descendants, are not iron-clad entities permitting no exceptions. In nature, organisms may respond with some traits to maximizing r , with others to bet-hedging. Both causal systems may operate at once, with different outcomes, on balance, for different traits. The concept of "tactic" as a coevolved assemblage of traits that must always be found together may prove misleading.

There is another, more serious, logical difficulty with most of the theoretical models reviewed in this paper, and with evolutionary theory in general. As Kempthorne and Pollak (1970) have pointed out, there are grave difficulties with the available mathematical definitions of fitness for sexual species. No fitness definition simultaneously accounts for sexual recombination, applies to whole organisms and their progeny rather than to populations of single genes, and allows for the different contributions of male and female offspring. Furthermore, fitness only applies to organisms in the context of a given environment. Therefore, an adequate definition of fitness must take into account the existence of different general environmental situations, and explicitly model the interaction of environment and organism. On these grounds, all theoretical work reviewed in this paper is suspect.

For example, theoreticians frequently argue as follows. Take a fitness measure (e.g., r or K) that can only be defined and measured on a whole population. Find out what combinations of biological traits will maximize that fitness measure. Then predict that we should expect individual organisms, or collections of individual organisms, to possess those optimal traits in the given situation.

One problem lies with the last step, which involves a theoretical feat akin to the statistical-mechanical derivation of thermodynamic laws from the behavior of individual molecules. Natural selection acts directly on individuals and their progeny, not on populations. Until we can establish that what holds for collections of individual organisms holds for the population (which we can measure) and vice versa—that what holds for the population holds for individual organisms—then the line of reason-

ing outlined above will remain suspect. The root of the problem lies in the need to define the fitness of individual organisms, and in the destruction of individual genotypes by sex.

For it makes no sense to speak of genotypes seeking to perpetuate themselves in a sexually reproducing population, since the processes of segregation and independent assortment of genes among the progeny continually break down and reshuffle the genotypes into new combinations. Since the individual organism acts for a multitude of genes, it does make some sense to speak of organisms seeking to perpetuate their genes, if not themselves. This compromise has logical faults, but seems to be the best we can do at present.

Because fitness has not been clearly defined for populations of sexually reproducing organisms, confusion arises when two people assume that they are both using the same, well-understood concept of fitness, when in fact they may not be talking about the same thing at all. To take an example, useful for its clarity but lacking subtlety, consider the confusion in a discussion of trends in reproductive effort when one participant assumes that organisms attempt to maximize r , and the other assumes that organisms attempt to minimize the probability of leaving no young at all. In fact, the focus is on the wrong object. Attention should be directed to the assumptions made about the definition of fitness, assumptions which should be tested along with the predictions that flow from them.

A less serious difficulty, easily avoided by learning some biology, arises frequently in discussions of the theoretical literature. All optimality models of evolutionary processes share a common weakness: natural selection favors not the optimal trait, but simply the best of the available traits. There is a world of difference between the optimal and the best available. We can be sure that selection will elicit a local optimum from the variability available in the ancestral population, but we cannot be sure that the result will match predictions made by a mathematical model that does not take the limits of natural variability into account.

Implications For Research

Of all the hypotheses reviewed above, I regard the following set as best supported by data.

In fluctuating environments, age and size at first reproduction should be respectively lower and smaller, reproductive effort higher, size of young smaller, and number of young per brood higher, than in constant environments, where the opposite trends should hold. We have a fair amount of field evidence, which is only suggestive, not conclusive, to indicate that these ideas should be worth testing experimentally (Gotto, 1962; Cody 1971; Gadgil and Solbrig, 1972; Price, 1973; Abrahamson and Gadgil, 1973); and there is one experiment that has confirmed several of the hypotheses for dandelions (Gadgil and Solbrig, 1972).

The field evidence consists of correlations between environmental patterns and reproductive trends. The arguments used are the "post hoc, ergo propter hoc" variety, and are less than convincing. Furthermore, although authors frequently invoke environmental instability to explain the trends they observe in life-history phenomena (e.g., Cody, 1966, 1971), no one has actually defined instability unambiguously, and then measured it along with the relevant reproductive traits during the process of selection.

Most broad comparisons of reproductive trends from field data lack proper control. Many investigators try to give evolutionary explanations of phenomena without eliminating possibilities that require no evolution at all. The proximal factor that most frequently confounds supposed evolutionary trends is food. Unless the nutritional state of the different populations has been assessed and corrected for, or the genetic basis of differences has been established through laboratory studies, then any assertion that a difference, observed in the field, has evolved and is an adaptation must be viewed with suspicion.

In order to make progress at this point, we need carefully controlled field experiments on a short-lived plant or animal. With the predictions of Table 4 in mind, the experimenter should contrast two sets of populations (replicates), one set living in a stable environment, the other set in a fluctuating environment. The experimenter should be sure to measure the fluctuations of relevant environmental variables, detail the biological mechanisms that mediate their impact on the population, and simultaneously measure age (if possible), size, number of young per brood, size of young, and reproductive effort. Since the experiment

should run for six to ten generations to detect a response to selection, it would probably run for two to three years if executed on a poeciliid fish in the tropics, for six months if executed on *Drosophila* in the laboratory, for six to ten years if executed on wild oats in country with a hard winter, or for twelve to twenty years if executed on pink salmon. *Drosophila* would take the least effort, but a poeciliid fish would provide the best analogy to larger fish and other vertebrates, and the results obtained would generalize more easily to economically important fish species.

The most exciting, recent, theoretical models make the assumption that reproduction costs something in terms of subsequent survival and future possibilities for reproduction (Williams, 1966a; Gadgil and Bossert, 1970; Schaffer 1972, 1974a; Charnov and Krebs, 1973). Predictions based on this idea depend on the shape of the relationship between reproductive effort at time t , and survival from time t to time $t + 1$. There are several approaches to measuring this curve, the most convincing of which involves manipulating the clutch sizes of a bird species that has a long period of parental care, and which does not put a large proportion of its reproductive effort into the production of an egg. If the experimenter could then measure the differences among treatments in adult survival to, and capacity to reproduce in, the next breeding season, we would have a reliable trade-off curve. A nesting colony of cliff swallows might present a good opportunity to do this if the adults returned to the same colony each year. Without such tests, the intriguing speculations of Williams (1966a, b), Gadgil and Bossert (1970), Schaffer (1974a), and Taylor et al. (1974) will remain unsubstantiated.

Correlational evidence from field observations will simply not substantiate a theoretical speculation, since an infinite number of models can be constructed that predict the same correlation. Only experiments can truly test theory. If we want knowledge of the natural processes that shape life histories, we will have to be willing to do experiments, even if they take years to execute. The alternative, a field full of interesting ideas supported in a broad way by correlational evidence, is not just unappealing—it isn't science.

Tests of predictions on reproductive trends may fail to give any information because the causal factors under study were complicated

by parameters affecting the behavior, genetics, or development of the population. I have some evidence from work in progress that this is the case for *Gambusia* and other poeciliid fish. Therefore, we need research that will start to establish the coevolutionary connections among reproduction, behavior, genetics, and development. Most theoretical models reviewed in this paper deal with females only and assume a stable age distribution. Natural populations are rarely in stable age distribution (Caughley, 1966), and the selective forces operating on males can be quite different from those operating on females (cf. Darwin, 1859; Trivers, 1972). Theoretical models should explicitly separate sexes and deal with both. Relaxing the assumption of a stable age distribution presents a more difficult problem; working out its implications is a job for someone less mathematically inept than I am.

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