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ENVIRONMENTAL UNCERTAINTY AND SELECTION FOR
LIFE CYCLE DELAYS IN OPPORTUNISTIC SPECIES

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Theoretical consideration of the evolutionary consequences of environmental uncertainty began with Dobzhansky's (1950) differentiation between tropical and temperate environments and the relative roles of physical factors in the determination of population numbers. Cole (1954) prompted interest in the evolution of life-history strategies with an inspection of the effects of changes in reproductive and survivorship patterns on the intrinsic rate of increase, r_m . Lewontin (1965) examined the sensitivity of r_m to changes in various life-history characteristics with the reasoning that the successful colonizing strategy would maximize the rate of growth of the population in the absence of density-dependent limitations. MacArthur and Wilson (1967) suggested that fitness is best described by the intrinsic rate of increase in the early stages of colonization, while the ability of the individual to utilize resources efficiently assumes increasing importance as the population becomes established. This notion of r - and K -selection was extended from the consideration of colonizing episodes and their evolutionary products to all populations, which when placed on a continuum of resource availability should exhibit the appropriate relative values of r and K (Pianka 1970). The utility of such a scheme may be questioned, however, because the selective conditions for life-history evolution are only assumed to relate to resource availability. Among the expected correlates of a catastrophic environment, in which density is rarely a major source of mortality, is rapid development followed by a brief prolific reproductive period.

Objections were raised by Hairston et al. (1970) regarding the use of population parameters r and K to describe the fitness of individuals, although their conclusions regarding general evolutionary trends do not contradict those of MacArthur and Wilson. Roughgarden (1971) and Charlesworth (1971) modeled the selection of life-history parameters (r and K) with conclusions similar to those described previously. The difficulty underlying their approach is that there is no specific character undergoing selection; rather, the phenotype is expressed only as its fitness, which approaches either r or K depending upon the density of the population. Their conclusions implicitly assume that all life-history characteristics will respond in the same direction to the same environmental events; i.e., that there exists one locus which controls all the reproductive and survival characteristics of the individual.

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The impact of environmental uncertainty has been implicated in the scheme of *r*- and *K*-selection, but only as an element that will maintain population levels below the carrying capacity. The predictability of juvenile survivorship is not necessarily a function of density. The possibility of such independence has led to the construction of models that contradict some of the expected correlates of *r*- and *K*-selection (Murphy 1968; Schaffer 1974). The potential for ambiguities and confusion when only one type of selective regime (resource availability) is considered was emphasized by Wilbur et al. (1974). They suggested further consideration of trophic level and environmental uncertainty as important factors in the determination of adaptive strategies.

The following treatment poses a set of environmental circumstances that are generally considered *r*-selecting conditions and examines their effects upon the evolution of a particular life-history characteristic. The constraints are identical to those proposed for the evolution of an opportunistic life history: exponential growth conditions which are occasionally interrupted by catastrophic density-independent mortality. I will deal with a hypothetical population that undergoes larval development in an environment which occasionally becomes totally unsuitable for survival, such as a water-filled tree hole or a temporary pool. In these instances catastrophic events could be considered droughts, in which all larvae die from desiccation.

Consider a population in which the eggs remain dormant until a sufficient stimulus has occurred. In the tree hole or temporary pool such a stimulus could be an elevated water level due to rainfall. If there is a polymorphic locus that determines the number of stimuli necessary for hatching, then the evolutionary consequences of environmental catastrophes could contradict the conclusions derived from the theory of *r*-selection.

THE MODEL

For simplicity I will deal with one locus and two alleles. Genotypes behave in the following manner: *AA*, hatching occurs immediately after the first environmental stimulus (early hatchers); *AB*, two such stimuli are required; *BB*, eggs will hatch only after the third stimulus (late hatchers). Although they will be referred to as eggs, the results of this model should apply to any developmental stage of genetically variable duration as long as the stage is not susceptible to the occasional catastrophes.

For reasons which will be discussed later, I assume that the population is semelparous and that reproduction occurs directly after adult emergence. This condition reduces the amount of time spent as an adult to a negligible fraction of the overall generation time. The semelparity, combined with the need for a hatching stimulus, creates a situation in which all individuals that hatch are vulnerable to the catastrophic event throughout the period of larval development. After numerous generations of random mating among adults, only the early-hatching genotype will remain entirely synchronous. Immediately after a stimulus, such as rainfall, the early-hatching genotype will consist entirely of larvae. The heterozygotes will be divided into two groups: those which have only been stimulated once, and are still eggs, and those which have just hatched after their second stimulus. The slow-hatching genotype (*BB*) will consist of three groups, hatchlings and eggs which

require one and two more stimuli before hatching. A catastrophe, such as desiccation, would eliminate all larvae if it occurred in the period of larval development following a hatching stimulus. This would be total mortality for genotype AA , but the cost to genotypes AB and BB would average only $\frac{1}{2}$ and $\frac{1}{3}$, respectively, due to the reserves of unhatched eggs. If there is mortality in the larval stage due to factors other than catastrophic events a proportion L will survive to reproduce under benign conditions. The average catastrophic mortality through time will be the average proportions of each genotype which are vulnerable to catastrophe multiplied by the probability (D) of a catastrophe occurring within the period of larval development. Thus, the average survivorship for each genotype will be for AA , $L(1 - D)$; AB , $L[1 - (D/2)]$; BB , $L[1 - (D/3)]$. If we define M as the average fecundity of all females in the population and L and M are independent of genotype, the net reproductive rate in the absence of catastrophes would be $L \times M$, which will be abbreviated as R_s . With catastrophes occurring periodically, the average net reproductive rate may be expressed as

$$R_0 = R_s(1 - D), \quad R_s[1 - (D/2)], \quad R_s[1 - (D/3)] \quad (1)$$

for genotypes AA , AB , and BB , respectively. Because there are differences in generation time this will not suffice as a definition of fitness. A statistic which will compare the performances of populations on the basis of net reproductive rate and generation time is

$$r_c = \frac{\ln R_0}{T}, \quad (2)$$

where the generation time is expressed as T . This expression is only an approximation of the intrinsic rate of increase, r_m (Andrewartha and Birch 1954). The accuracy of the approximation depends upon the magnitude of the finite rate of increase R_0 and the duration, relative to the generation time, of the reproductive period. It is an exact determination of r_m when a synchronized semelparous population is considered. For iteroparous populations, or those with variation in age of reproduction, the percentage difference between r_m and r_c increases with R_0 . However, for populations with R_0 less than 10^3 and reproductive periods of less than 30% of the total generation time, r_c will not deviate from r_m by more than about 2% (Laughlin 1965). Because of these discrepancies, the hypothetical population in this model is confined to semelparity with immediate reproduction at maturity, although these constraints could be relaxed somewhat with no major changes in the general conclusions, particularly when R_0 is less than 10^3 .

I propose the extension of equation (2) to the genotypic level. Fitnesses will be defined as the rates of growth for hypothetically isogenic populations of all genotypes, so that the fitness of the i th genotype is defined as

$$m_i = \frac{\ln R_0(i)}{T_i}. \quad (3)$$

Because the actual units of time are arbitrary, T_i can be expressed in terms relative to the genotype with the shortest generation time. If a denotes the average period of

time between stimuli, the fitnesses can be described by the following equations:

$$\begin{aligned} m_{AA} &= \ln [R_s(1 - D)], \\ m_{AB} &= \frac{\ln \{R_s[1 - (D/2)]\}}{1 + a}, \\ m_{BB} &= \frac{\ln \{R_s[1 - (D/3)]\}}{1 + 2a}. \end{aligned} \quad (4)$$

I will now consider a special case in which the generation time of genotype *AA* has evolved to track the hatching stimuli through time. That is, *a* approximates 1. This allows the following algebraic simplification:

$$\begin{aligned} m_{AA} &= \ln [R_s(1 - D)], \\ m_{AB} &= \frac{1}{2} \ln \left[R_s \left(1 - \frac{D}{2} \right) \right], \\ m_{BB} &= \frac{1}{3} \ln \left[R_s \left(1 - \frac{D}{3} \right) \right]. \end{aligned} \quad (5)$$

Assuming random mating among all genotypes and a large enough population to avoid random changes in gene frequencies, a stable polymorphism will exist when $m_{AA} < m_{AB} > m_{BB}$, or

$$\ln [R_s(1 - D)] < \frac{1}{2} \ln \left[R_s \left(1 - \frac{D}{2} \right) \right] > \frac{1}{3} \ln \left[R_s \left(1 - \frac{D}{3} \right) \right]. \quad (6)$$

Solving both inequalities for R_s ,

$$\frac{1 - (D/2)}{(1 - D)^2} > R_s > \frac{[1 - (D/3)]^2}{[1 - (D/2)]^3}. \quad (7)$$

The region of stable polymorphism is obtained from the intersection of the region below the function $R_s = [1 - (D/2)]/(1 - D)^2$, and the region above the function $R_s = [1 - (D/3)]^2/[1 - (D/2)]^3$. The shaded area in figure 1 depicts the combinations of R_s and D that will result in a stable polymorphism. Combinations of R_s and D above this region lead to the fixation of allele *A*. Those below the region result in the fixation of the late-hatching allele *B*. It should be evident from inspection that fixation of the early-hatching allele becomes less likely with an increasing probability of catastrophe.

If \hat{q} denotes the frequency of the late-hatching allele at genetic equilibrium, the mean fitness of the population becomes

$$\bar{W} = (1 - \hat{q})^2 m_{AA} + 2\hat{q}(1 - \hat{q})m_{AB} + \hat{q}^2 m_{BB}. \quad (8)$$

However, the intrinsic rate of increase of the population is defined as the rate of growth of a population when the birth and death rates are constant through time. This would be a function of R_s , each genotypic generation time, and the relative proportions of genotypes in the following manner:

$$r_m = (1 - \hat{q})^2 \ln R_s + 2\hat{q}(1 - \hat{q}) \frac{\ln R_s}{2} + \hat{q}^2 \frac{\ln R_s}{3}. \quad (9)$$

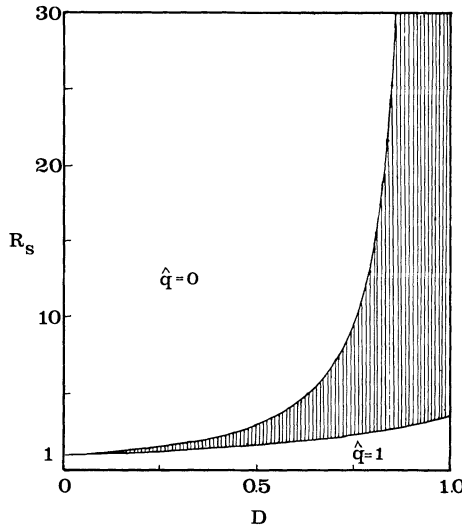


FIG. 1.—Evolutionary consequences of combinations of the net reproductive rate in the absence of catastrophes (R_s) and the probability of catastrophe, D . Conditions for a stable polymorphism are depicted by the hatched area. The \hat{q} represents the frequency of the late-hatching allele.

The effect of the frequency of the late hatching allele on the intrinsic rate of increase is obtained from the derivative of equation (9) with respect to \hat{q} ,

$$\frac{\partial r_m}{\partial \hat{q}} = \left(\frac{2\hat{q}}{3} - 1 \right) \ln R_s, \tag{10}$$

which is negative for all values of q between 0 and 1. Here is a situation where environmental harshness favors the genotype with the longer generation time, allowing a reduction in the intrinsic rate of increase.

Under conditions allowing a polymorphism to persist the frequency of the late-hatching allele will be $\hat{q} = (m_{AB} - m_{AA}) / (2m_{AB} - m_{AA} - m_{BB})$, or

$$\hat{q} = \frac{(1/2) \ln \{R_s[1 - (D/2)]\} - \ln [R_s(1 - D)]}{\ln \{R_s[1 - (D/2)]\} - \ln [R_s(1 - D)] - (1/3) \ln \{R_s[1 - (D/3)]\}} \tag{11}$$

$$= \frac{\ln \{[1 - (D/2)]^{1/2} / (1 - D)\} - (1/2) \ln R_s}{\ln \{[1 - (D/2)] / (1 - D)[1 - (D/3)]^{1/3}\} - (1/3) \ln R_s} \tag{12}$$

We may now examine the effects of changes in mortality (due to factors other than catastrophe) and fecundity on the equilibrium gene frequencies. The following notation will simplify the succeeding derivation. Let

$$E = \ln \frac{[1 - (D/2)]^{1/2}}{(1 - D)} \quad \text{and} \quad F = \ln \frac{[1 - (D/2)]}{(1 - D)[1 - (D/3)]^{1/3}}$$

so that

$$\hat{q} = \frac{E - (1/2) \ln R_s}{F - (1/3) \ln R_s} \tag{13}$$

Taking the partial derivative of \hat{q} with respect to R_s , we obtain

$$\frac{\partial \hat{q}}{\partial R_s} = \frac{(3/R_s)(6F - 2 \cdot \ln R_s) - (2/R_s)(6E - 3 \cdot \ln R_s)}{4(3F - \ln R_s)^2}. \quad (14)$$

The $\partial \hat{q} / \partial R_s$ is positive when the numerator in equation (14) is positive, generating the inequality

$$\frac{3}{R_s} (6F - 2 \cdot \ln R_s) > \frac{2}{R_s} (6E - 3 \cdot \ln R_s), \quad (15)$$

which reduces to $18F - 6 \cdot \ln R_s > 12E - 6 \cdot \ln R_s$, or $3F > 2E$. Upon resubstitution, this expands to

$$\left\{ \frac{1 - (D/2)}{(1 - D)[1 - (D/3)]} \right\}^3 > \left[\frac{1 - (D/2)}{(1 - D)} \right]^2. \quad (16)$$

This inequality holds for all D between 0 and 1. That is, a change in the environment that enhances the noncatastrophic net reproductive rate should select for a higher proportion of individuals that exhibit delayed hatching.

DISCUSSION

Biogeographical hypotheses may now be raised. Suppose the species expands its range beyond that of a predator, yielding a higher larval survivorship in the area of colonization. If the probability of catastrophe in this area remains the same, equation (14) would predict that a higher proportion of late-hatching individuals should occur in the new habitat. The increase in R_0 would have to be substantial to prevent a decline in r_m due to the increased generation time.

Although the model allows a possible decline in the intrinsic rate of increase in such a situation and a certain decline in the case of increased environmental uncertainty, it assumes that larval survivorship and fecundity are not concurrently undergoing selection. As such, this model should not be construed as a direct contradiction to the hypotheses generated by the theory of r -selection. Instead it illustrates a possible exception to the generalities. It is still possible for r -selection to occur, but only if genes which permit early hatching are closely associated with genes that contribute to the survival and fecundity of the individual. In fact, this model provides an avenue by which the concept of r -selection can be partially tested. Given a population in which there is genetic variation in generation time, R_0 for the offspring of rapid individuals must be much larger than that of delayed individuals for r -selection to occur at all.

Variation in generation time may arise from differential responses to hatching stimuli as in this example, or from variable responses to stimuli that reinitiate development after diapause. It may also arise through variable entry into a dormant state if some individuals reproduce instead of entering diapause. Such phenomena have been frequently observed in *Aedine* mosquitoes that occupy ephemeral habitats. Gillette (1955a, 1955b) determined that hatching response in *Aedes aegyptii* is genetically controlled. Istock, Zisfein, and Vavra (1976) demonstrated considerable variation in development time and diapausing tendencies in the pitcher plant mosquito, *Wyeomyia smithii*. A dimorphism for the tendency to enter a summer

diapause is postulated as a basis for highly imperfect tracking of resources through time (Istock, Vavra, and Zimmer 1976). This model may help to explain the evolution of the phenomenon. Danilievski (1965) documents numerous examples of the genetic determination of phenological phenomena. In the Odonata, variation in length of diapause causes a mixture of univoltine and semivoltine life cycles in some species (Corbet 1957; Eller 1963; Lutz and Jenner 1964), although genetic control of this phenomenon has not been demonstrated. Natural historians have never been particularly puzzled by such observations, but their implications in the evolution of life-history parameters have been overlooked.

The major conclusion to be drawn from this model concerns the feasibility of predicting the selective effects of environmental variables upon a population parameter r_m . The direction and magnitude of evolutionary response can only be predicted when the response of each character affecting this parameter is known. The possibility that separate components of r_m will respond in opposing directions creates a potential for ambiguous predictions. Wilbur et al. (1974) describe a number of these, concluding that predictions about selection on life-history characteristics are incomplete or oversimplified when they are made solely on the basis of a resource continuum. This model illustrates the risks involved in modeling selection on r_m and not on its components, which are based on phenotypic characters. Broad conclusions about the response of r_m to environmental variables must await the results of direct experimentation.

SUMMARY

A model is presented which considers genetic variation in the duration of egg dormancy in populations occupying larval habitats that occasionally become entirely unsuitable. The probability of such a catastrophe and the net reproductive rate in the absence of catastrophes (and in density independent conditions) determine the conditions required for fixation of either the early- or late-hatching allele. The model shows that a more catastrophic environment will favor the late-hatching allele, presenting the possibility for a decline in r_m with an increase in environmental uncertainty. The implications of this result to the concept of r -selection are discussed, and examples of systems where the model could apply are presented.

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