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# Environmental fluctuations: How do they affect the topography of the adaptive landscape?[†]

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**Abstract.** A Phenotypic Adaptive Landscape is defined with fitness as the ordinate, and longevity of the juvenile phase and duration of disturbances to the adult phase as the horizontal axes. The effect of local environmental perturbations on the landscape's shape is studied using a semistochastic population model. In this model the intrinsic population dynamics takes the form of a differential-delay nonlinear equation and the environmental disturbance appears as a multiplicative *telegraphic noise*. We demonstrate that the landscape has no single characteristic scale. Rather, it shows adaptive peaks corresponding to an integer relation between the biological and the environmental periodicities. Since the system is constrained by a finite time and a finite physiological range, the landscape may have different topographies for different local environmental regimes. A very simple fully deterministic model is presented, predicting landscapes that are similar to those obtained by the semistochastic model. Application to life history strategies are discussed.

**Keywords.** Telegraphic noise; environmental disturbances; biological periodicity; life-cycle parameters; nonlinearity; stasis.

## 1. Introduction

"The basic viewpoint of population genetics is . . . that large populations tend to be heteroallelic at all loci and strongly so at many. Mathematically, the species is thought of as located in a point in a gene frequency space with $(k_i - 1)$ dimensions, $k_i$ being the number of alleles at the $i$th locus and summation being over all loci. Evolution consists of movement in this space" (Wright 1969, p. 472). This assertion, simplified for pedagogic reasons to the two-dimensional case (Wright 1932), is usually termed the "Sewall Wright Landscape" (SWAL). It has become the single most suggestive metaphor in speculative evolutionary theorization.

Another metaphor which has been of enormous significance is that of the multidimensional niche space, popularized by Hutchinson (1957) and his students. The focus of the niche metaphor is the interface between organisms considered phenotypically and the properties of their environment. Just as there was a pedagogic simplification of Wright's image to two dimensions, so the Hutchinsonian niche is pedagogically simplified to a small number of dimensions.

Many of the speculative theories that have developed in the fields of ecology and evolution in the past thirty years can be seen as attempts to crystalize the interplay between these two metaphors. Lewontin (1974) has represented this interplay

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diagramatically as a paired set of surfaces, one set representing the genotype, the other the phenotype, the individual surfaces in each set representing different temporal manifestations. Arrows, representing developmental and environmental events and their interactions, connect the genotype at a particular time to the phenotype at the next time, and arrows, representing reproduction, connect that phenotypic surface to the temporally subsequent genotypic surface. The point of the diagram is to emphasize the difficulty of constructing meaningful theories of either phenotype or genotype change.

The two main methods of attempting to circumvent these difficulties have been to make many simplifying assumptions ("Ceteris Paribus", Ben Leib 1980), or to redefine the problem. In the first case simpler metaphors are constructed which may themselves prove fruitful (Greenwood *et al* 1985, p. vii). In the second case, authors may say that they are dealing with either the SWAL or the Hutchinsonian Niche when in fact they are not. Many curious theories have therefore appeared in the literature under these names, occasionally several in one publication. For example, on page 167 of Dobzhansky *et al* 1977, the authors accept Wright's assertion that the ordinates of an adaptive landscape represent the frequencies of two alleles. In this definition each point on the adaptive landscape corresponds to a population of organisms. On page 168 these authors say that "the summit of the genetic peak is held by . . . the genotypes that are fittest in the environment in which the species lives." That is, populations characterized by *gene frequencies* are replaced by individuals characterized by *genotypes* within the space of two consecutive pages of the same work. This example of shift of meaning of the basic metaphor of the adaptive landscape is by no means unique or original. These difficulties and pitfalls do not excuse us from attempting theoretical clarifications of the interface between evolution and ecology. If the problem at issue is sufficiently clearly defined, predictive theory is possible. Clarity of definition can arise either from choosing very simple organisms (Slobodkin 1986) or by choosing clearly delimited characteristics which are shared by many kinds of organisms.

Recently there has been concern with trajectories on the metaphorical adaptive landscape, and more specifically with the rate of transition between peaks which are connected by a single-minimum valley (Newman *et al* 1985; Lande 1985); a cross-section of the adaptive landscape is taken as representing the mean fitness of the population plotted against some genotypic or phenotypic states of the system, and the environment is taken as constant. In the present work we focus on shape changes in adaptive landscapes due to environmental fluctuations. In particular we will show that the frequency of local disturbances may determine the landscape's topography.

We will not use the adaptive landscape used by Wright, since our concern is evolution of phenotypes, rather than gene frequency change. Our phenotypic adaptive landscape (PAL) has contours of fitness on a surface of phenotype and environment, and the entities at issue are individual organisms differing in phenotype. Our representation also differs from the customary presentations. By choosing a single environmental variable and a single phenotypic response, we represent in three dimensions phenotype, environment and fitness. Our primary inference will be that certain complex conclusions can arise from this system. Certainly, a more complex presentation will not yield any simpler results.

We have specifically focused concern on properties of time, which are of great generality. The biological property whose adaptive landscape will be explored here is the duration of a juvenile life stage that is resistant to environmental disturbances. In our model this duration appears as a time-delay in the system representing the biological period – the generation time. Environmental change occurs as a series of disturbances forced on the population. The effects of this type of forcing may not be unique to organisms with complex life-cycles, whose different life stages differ in susceptibility to deleterious environmental conditions. Rather, adaptive landscapes described here may also be relevant to other internally periodic biological processes that are subject to external pulsating forcing.

## 2. The basic model

Our basic model is a semi-stochastic equation. The deterministic part of the equation describes a continuous growth of a single homogeneous population with overlapping generations in a restricted environment. The birth process is assumed to have two stages: birth of juveniles, and recruitment of juveniles to the adult population; recruitment is the only density dependent element in this system. The environment is characterized by what is called *telegraphic noise*, that is alternating harsh and favourable episodes. Harsh episodes take the form of disturbances that completely obliterate all adults during the time, $\delta$, in which each disturbance prevails. The duration of the intervals between disturbances is assumed to be an exponentially distributed random variable with a mean, $\omega$. It is useful to cast the resulting dynamics of the system in the form

$$x'(t+\Delta t) = \{x'(t) + \lambda' x'(t-\tau)[1 - x'(t) - \mu x'(t)]\}\,[1 - D(t)]\,\Delta t. \tag{1}$$

Here $x(t)$ stands for the number of adults at time, $t$, and $x'(t) = x(t)/K$, where $K$ is the carrying capacity of the environment. $\lambda'$ stands for the reproductive rate, containing an element of juvenile mortality, so that

$$\lambda' = \lambda \exp(-\mu'\tau),$$

where $\lambda$ is the birth rate, $\mu'$ is the mortality rate of juveniles whose life span is $\tau$. $\mu$ stands for the mortality rate of adults, and $D(t)$ is the environmental process, assuming the values 0 and 1. The transition from $D(t) = 0$ to $D(t) = 1$ occurs with probability, $1/\omega$, while the inverse transition occurs $\delta$ time units later (for full details of this model see Agur 1985; Agur and Deneubourg 1985). Average population fitness is measured as the average number of offspring per individual.

To follow the potential evolutionary trajectory in different habitats we plot the biological parameter of interest, here the juvenile life-span, $\tau$, and the environmental parameter of interest, here the duration of the disturbance episode, $\delta$, on a horizontal plane, called the system surface. Each system surface represents a set of environments – a habitat – of a given disturbance frequency, $1/\omega$. Each point on the system surface represents a population of a single type characterised by its juvenile life span, in an environment whose characteristic disturbance duration is $\delta$. Population dynamics is simulated according to (1) for each point on the system surface. The obtained fitness values are represented as points on a perpendicular axis directly above the corresponding points on the system surface. The interconnected group of all fitness points over the entire surface forms a top surface, representative of the potential evolutionary landscape. Humps in the top surface represent locally optimal types, when the largest hump for a given environment is expected to be globally optimal in that environment. Figures 1–3 represent the adaptive landscapes of three habitats differing in the local disturbance frequency. The range of $\tau$, representing some physiological species range, is similar in the three sets, and so is the range of $\delta$ representing environmental change over some geological period. In general, maxima in the adaptive landscape appear when the relation between the biological period and the environmental period is an integer, that is, when one period is a multiple of the other. However, when the landscape is constrained by a fixed range in $\tau$ and $\delta$, differences in local disturbance frequency appear to have an important qualitative impact on the landscape's topography; on the number of adaptive peaks available for the species, on the height of the peaks and the depth of the valleys, on the smoothness of the landscape, and on the curvature of the peaks and valleys.

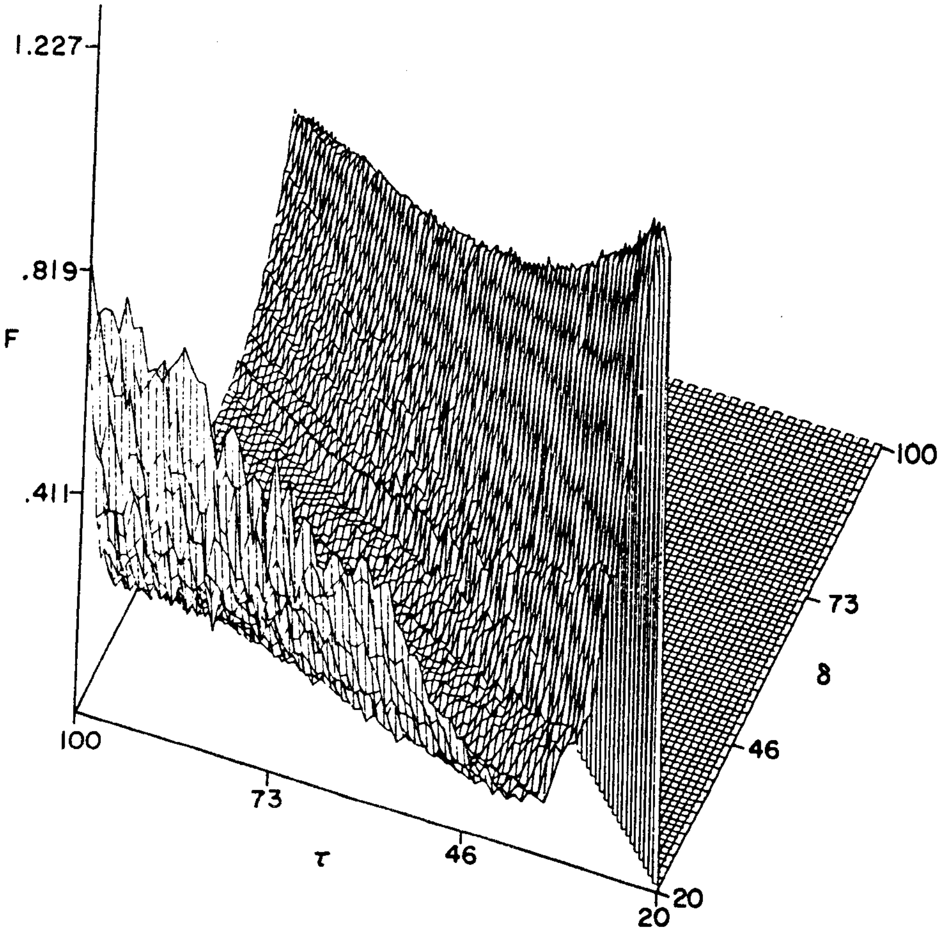

**Figure 1.** The phenotypic adaptive landscape for environments with low frequency of disturbances; the average duration of the disturbance-free interval is, $\omega = 40$. Average population fitness, $F$, is calculated by simulating (1), where $\lambda' = 1$, $\mu = 0$, $\delta$ is the duration of the disturbance period and $\tau$ is the longevity of the resistant life phase.

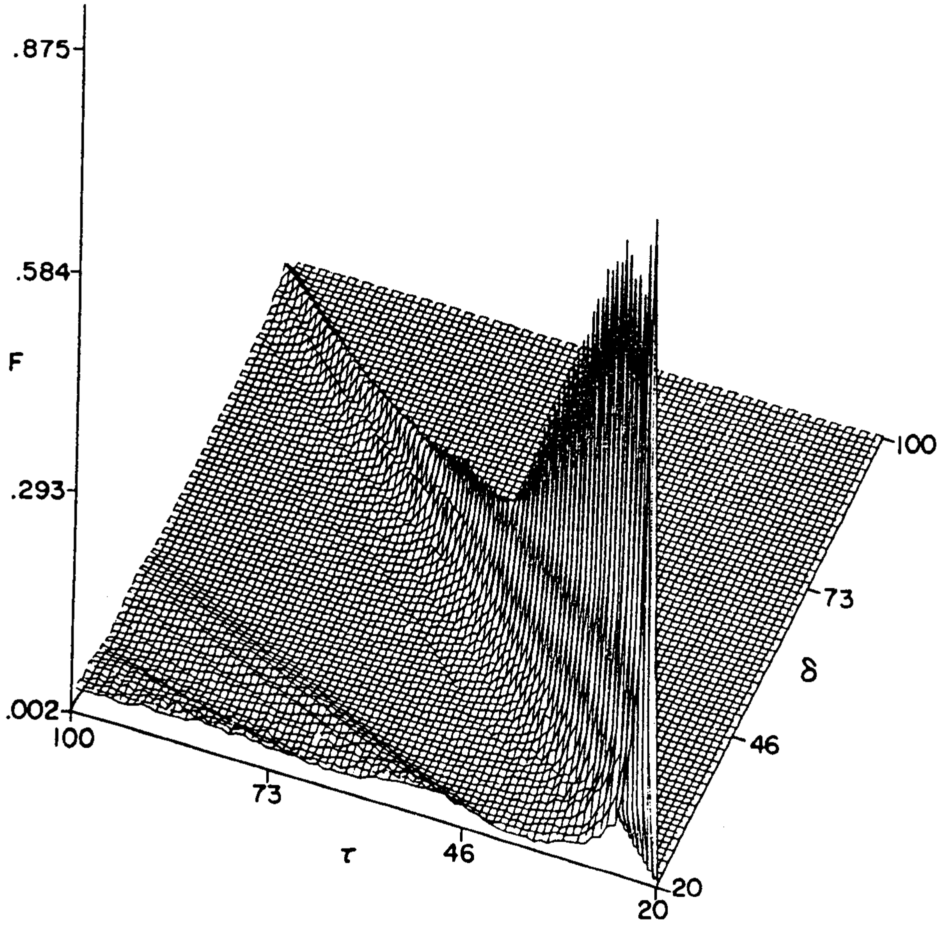

**Figure 2.** The phenotypic adaptive landscape for environments with an intermediate frequency of disturbance; the average duration of the disturbance-free interval is, $\omega = 20$. Other parameters as in figure 1.

## 3. Analysis of the model

In order to account for the relation between the frequency of the environmental disturbance and the topography of the adaptive landscape, and since the basic model is intractable in its semi-stochastic version of (1), we make some further simplifying assumptions. In the simplified model we assume that in harshly varying environments various details of the intrinsic population dynamics, such as density dependence, do not find expression and therefore can be ignored altogether. As a result the population dynamics can be described as a one-dimensional process on the time axis (Agur 1985). Since in our basic model adults are assumed to have a constant birth rate, the phenotypic fitness should be positively related to the average duration of the period in which adults prevail in the system, $F'$.

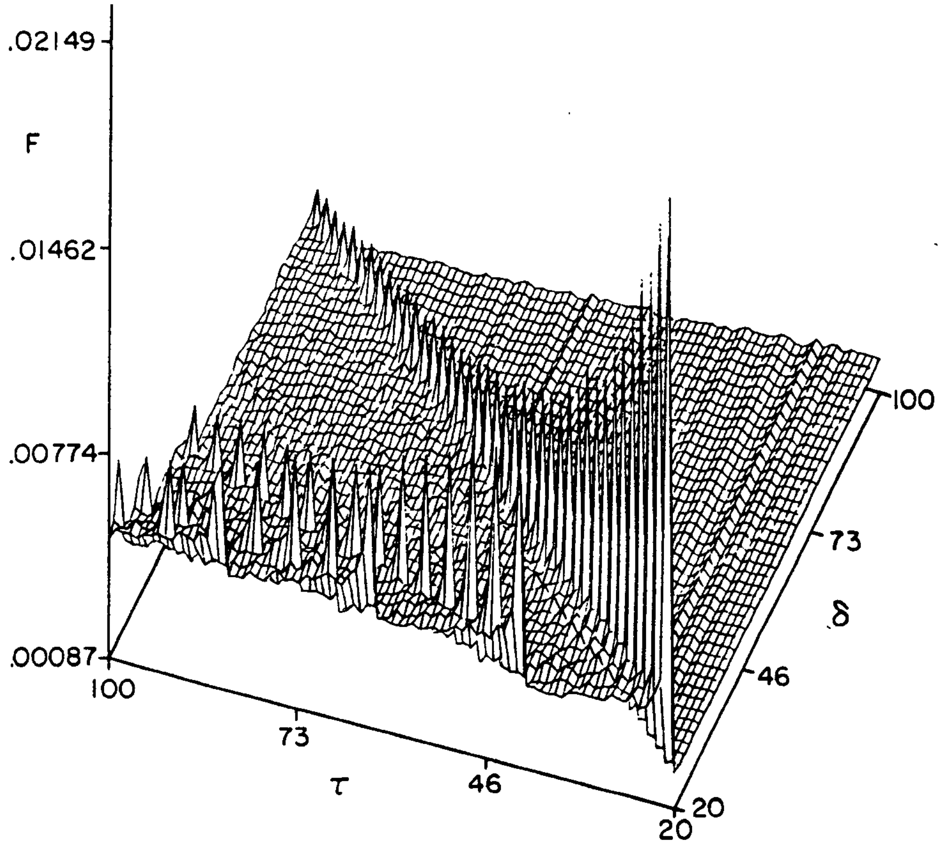

**Figure 3.** The phenotypic adaptive landscape for environments with high frequency of disturbance. The average duration of the disturbance-free interval is, $\omega = 1.1$. Other parameters as in figure 1.

In a fully periodic system $F'$, measured over a period of $n$ generations, is given by

$$F = \begin{cases} \frac{N}{n}\sum_{i=1}^{n}(i-1)[N(\omega+\delta)-\tau]+\omega & \text{for } N(\omega+\delta) < \tau < N\omega+(N+1)\delta; \\ N\omega & \text{otherwise.} \end{cases} \quad (2)$$

$N$ is the relative time scale (Agur 1985) so that

$$N = [\tau/(\delta+\omega)],$$

($N = 1$ for $\tau < \delta + \omega$). The point

$$\tau = (N-1)\omega + N\delta, \quad (3)$$

in (2) is a point of discontinuity where $F'$ goes from minimum to maximum; as $\tau$ increases beyond this point $F'$ decreases nonlinearily until it reaches a new minimum. The points defined by (3) are thus points of instability where small changes in $\tau$ will cause a large change in fitness. The number of instability points in our model gives the number of adaptive peaks available for the species. For given ranges of $\tau$ and $\delta$ the number of adaptive peaks increases with increasing frequency of disturbance, $1/\omega$.

For $\tau = 20$ to $\tau = 100$ and $\delta = 20$, the adaptive peaks are expected, according to (3), to be located on $\tau = 20, 41, 62, 83$ for $\omega = 1$, on $\tau = 20, 50, 80$ for $\omega = 20$, and on $\tau = 20$, 80 for $\omega = 40$. It is interesting to note that these results for the fully periodic environment are in agreement with the simulation results of (1) for the stochastic occurrence of the disturbance (figures 1–3). Hence the very simple deterministic model accounts for the behaviour of the seemingly elaborate semi-stochastic model in (1). The effect of stochasticity, in figures 1–3 is to "smear" the adaptive landscape; as $N$ increases more disturbances are allowed to occur within one generation and the random element becomes more meaningful; hence the concurrent decrease in height of peaks and depth of valleys with increasing $N$ in figures 1 and 2.

When disturbances occur at random, $F'$ is given by

$$\begin{aligned} F' &= \omega'(1)p(i = 1) + [\omega'(1) + \omega'(2)]p(i = 2) \\ &\quad + [\omega'(1) + \omega'(2) + \omega'(3)]p(i = 3) + \ldots \\ &= E(\omega') \sum_{j=1}^{\infty} jp(i = j), \end{aligned}$$

where $\omega'(i)$ is the duration of the breeding season in generation $i$, and $p(i)$, is the probability of population extinction in generation $i$. But the probability of extinction of the process in each generation is independent of its history.

Hence

$$\begin{aligned} p(1) &= p, \\ p(2) &= p(1-p), \\ p(3) &= p(1-p)^2, \\ &\vdots \\ p(i) &= p(1-p)^{i-1}, \end{aligned}$$

where $p$ is the extinction probability in any generation. According to the rules of the Poisson process

$$E(\omega') = \omega.$$

Hence,

$$F' = \omega \sum_{j=1}^{\infty} p(1-p)^{j-1} = \omega/p. \tag{4}$$

For

$$2\delta \geqslant \tau > \delta, \tag{5}$$

$p$ is given by (Agur 1985)

$$p = 1 - \exp[-(1/\omega)(\tau - \delta)][1 - (1/\omega)(\tau - \delta)]. \tag{6}$$

Putting (6) in (4) and deriving with respect to $\tau$, it can be shown that in the region defined by (5) $F'$ decreases with increasing $\tau$ for constant $\delta$ and $\omega$; derivation with respect to $\delta$ with $\tau$ and $\omega$ being constant shows that $F'$ increases with increasing $\delta$, that is with increasing environmental harshness. This, admittedly limited, analysis of the stochastic case is consistent with the analysis of the fully periodic case and with the simulation results.

## 4. Discussion

Our main purpose in this work was to show that local environmental perturbations can affect the topography of the adaptive landscape, and hence, evolutionary patterns. To this end we used a logistic type deterministic population model with a superimposed stochastic environmental disturbance in the form of a multiplicative *telegraphic noise*. This model which was originally constructed to describe the dynamics of marine intertidal populations (Agur and Deneubourg 1985), has many different applications, some of which will be mentioned below. The approach presented here is novel in considering explicit forms of the population dynamics and of the environmental change as the basis of formation of the adaptive landscape. It should be noted that for simplicity, competition among different phenotypes has not been considered in the model; our assumption is that the phenotype belonging to a homogenous population with the highest average fitness in a given environment is the optimal type in that environment (Agur 1983).

We have shown that there exists a universal landscape with adaptive peaks coinciding with the integer relation between the biological and the environmental periods. However, this universal landscape *has no characteristic scale*; its shape, namely the height of the peaks, the distances between them and the topography curvature depend on the relationships between the population and the environmental periodicities. Since our concern is with a finite evolutionary time, and hence with a finite geological scale and a finite physiological scale, our system is not infinitely flexible. Rather it is *locked* within the boundaries of these two scales. As a result the landscape "visited" by the populations during evolutionary time is completely different in different environmental regimes.

Regardless of the frquency of the disturbances, a juvenile life span just slightly longer than the disturbance duration has maximum fitness. It guarantees that some adults will have a maximal time for reproduction prior to being eliminated by the next disturbance. In addition to this peak in the adaptive landscape, other lower topographic features are seen which vary with disturbance frequency and represent complex harmonics of the system (in the sense of Oster and Takahashi 1974). If the disturbances are of sufficiently low frequency the pattern consists of a single trough with a ridge in fitness at the poles of the physiological range of the species (figure 1). At intermediate frequencies of disturbance there are several more flat ridges protruding from the main valley (figure 2). At very high frequencies of disturbance these ridges resolve into a series of spikes (figure 3). That local environmental fluctuations affect the shape of the *locked* adaptive landscape is thus our main conclusion. From these results there emerges the possibility that low disturbance frequency (figure 1) may favour gradual evolution; high disturbance frequency (figure 3) may favour discontinuous phenotypic evolution, while under intermediate disturbance frequency (figure 2) a large range of environmental changes may have little effect on the population fitness, hence favouring *stasis*.

Our results bear upon a central problem in ecology, namely, that of life history strategies and the co-ordination of temporal biological properties with those of environmental perturbation. Discussions of this problem have focused on which kinds of response mechanisms should be used for dealing with different durations of disturbance. For example, it has been suggested that genetic change is inappropriate as a response to successive and repeated seasonal alterations (Levins 1965) and, in general, short term reversible response mechanisms are most suitable to short term reversible environmental events (Slobodkin 1968; Slobodkin and Rapoport 1974). The problem takes on particular interest in organisms with clear ecologically distinct life stages. How should the temporal properties of one stage evolve in response to properties affecting some other stage?

We have focused on the situation in which there are two life stages, one subject to destruction by intermittent environmental pressures of fixed duration, the other with a reasonably short fixed life expectancy. There are two ways in which this can be imagined. The sensitive stage may be the young or the adult. If the young are sensitive then an extension or repetition of the breeding season for the adults is perhaps the only way to survive. For example, in cod, oysters and many other marine animals, the eggs and larvae are extremely sensitive to environmental conditions, so that many or even most breeding seasons result in a negligible number of recruits to the adult population. However, the adults live to reproduce during as many as fifteen or twenty reproductive seasons, at least one of which is quite likely to be favourable (Beverton and Holt 1957). In these cases there is clear selective advantage to enhanced longevity of the adult life stage.

There is a fundamental asymmetry between the situation in which adults evolve to circumvent deleterious periods for their young and that in which young evolve to circumvent deleterious periods for the adults. In the first case, the adults can be thought of as spreading their reproductive effort by holding their life-time supply of gametes a bit longer and releasing them a few at a time. The young, however, must make an-all-or-none commitment; maturation can only occur once. In many plant species, most notably annuals and biennials, but even including some perennials, the adults are relatively short-lived and may or may not set seed in any particular year, but the seed bank may persist in producing new young plants for many years (Martins and Jain 1979). In these cases polymorphism in longevity of the seeds ensures that new attempts are made to establish plants each season and some of the seasons are likely to prove favourable. We have shown that, if the adults are sensitive and the variance of developmental time of the young is relatively small, then the period of juvenile life should be just slightly longer than the episode of environmental duress on the adults, or a multiple of the characteristic environmental period. In other words, the durations of life stages may be rationalized by considering the environment of an entirely separate life stage.

A diapausing insect pupa or a dormant seed of an annual plant is proceeding with development at a much slower pace than would be dictated on biochemical or physiological grounds. To what extent are the rates of development in other organisms determined by the temporal environmental parameters?

Further, on the level of relatively rapid sequences of physiological and behavioural events, it has already been suggested that time constants are expected to relate to the temporal environment (Slobodkin and Rapoport 1974). We are now suggesting that the timing of sequential physiological processes may relate to temporal patterning of the internal or external environment as it affects the other stages in the sequence. As sequential processes are predominant in developmental biology our analysis implies that the duration of some of these processes in some organisms may be a consequence of evolutionary and ecological limitations. That is to say that the patterning of environmental perturbations may select for different durations for developmental stages; particular stages may be speeded up or slowed down by natural selection in response to differing susceptibilities to environmental perturbation acting on other developmental stages.

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