

What is bet-hedging?

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1. Introduction

It is often said that 'A bird in the hand is worth two in the bush'. On one interpretation of this saying, the bird in the hand must be released before those in the bush can be pursued, and the probability of catching both free birds is taken to be smaller than the probability of catching neither. Thus, the hunter would do better, on average, to keep the bird already in hand. But there is a second, more interesting interpretation, according to which the probability of success is taken to be large enough that the hunter would actually end up with more than one bird, on average, by dropping the bird already captured and pursuing the two free ones. In this case the point of the saying would be that the advantage of ending up with two birds (even most of the time) may not offset the disadvantage of ending up with none (even some of the time). This implies that the *variance* of success may need to be weighed against the *average* success, to determine which hunting strategy is better. A similar logic seems to inform the equally common 'Don't put all your eggs in one basket', a warning that is taken seriously by the managers of investment portfolios. Likewise, insurance policies cost more than they are expected to return in the form of benefits, so on average they reduce the wealth of those who purchase them. But they also reduce the *variance* of wealth, by preventing all-out financial disasters. These examples suggest that people often speak and act as if they believe that they should 'hedge their bets'.

Given this belief, it seems natural to ask whether plants and animals ever sacrifice some of their potential fitness in order to reduce their probabilities of complete failure. In other words, is there an evolutionary trade-off between *expected* fitness and the *variance* of fitness? A substantial theoretical literature says that there is, under certain circumstances. Here, we briefly review the growth of this idea and show why it works *only* 'under certain circumstances'. Many different patterns of behaviour, development, and polymorphism have been interpreted as 'bet-hedging'. We attempt to distinguish among these, and we emphasize that only some of them actually involve trade-offs between the mean and variance of fitness. We argue that, even where environmental variation promotes genotypic or phenotypic polymorphisms, such polymorphisms can seldom be correctly interpreted as evidence of adaptive bet-hedging. We then illustrate some of these issues by discussing a simple bet-hedging model for the diapause strategies of partially bivoltine insects living in temporally variable environments.

2. Polymorphism, coexistence, and adaptation

The concept of bet-hedging has appeared, in different forms and under different names, in the literatures on population genetics, ecology, and life-history theory. Felsenstein (1976), Hedrick *et al.* (1976), Christiansen (1974, 1985), and Walsh (1984) review a range of genetic models in which variable selection and migration lead to the maintenance of genetic polymorphism. Chesson (1985, 1986), Warner and Chesson (1985), and Chesson and Case (1986) review a class of ecological models in which environmental variation can promote the coexistence of species. Schaffer and Gadgil (1975), Giesel (1976), Stearns (1976, 1977, 1982), Rubenstein (1982), Bulmer (1984, 1985), Goodman (1984), and Kaplan and Cooper (1984) review models for the evolution of life histories in variable environments, where the best reproductive strategy may involve a probabilistic phenotype.

Stephens and Krebs (1987) review models of foraging behaviour in which the variance of net energy gain is often as important as its average, so that an individual's best *foraging* strategy may involve short-term 'bet-hedging' with respect to a currency such as energy. But the ultimate goal of most foraging strategies is to *maximize* the individual's *expected fitness*, which is measured in a currency different from energy. A similar issue surrounds brood reduction in birds, which is often interpreted as bet-hedging (e.g. Mock 1984). In obligate brood reduction (the common form in raptors), the female lays two eggs, but only one offspring is ever reared to fledging. If both eggs hatch, the older sibling invariably kills the younger one, but often only one of the eggs actually hatches (owing to egg infertility or inviability). Brood reduction in this case is seen as a form of 'insurance'. In facultative brood reduction, females lay more eggs than they are able to rear in most years, but when food is plentiful, all the young may fledge. This is seen as parental bet-hedging in the face of an unpredictable and highly variable food supply. In both cases, the argument is that parents will on average *increase* their number of fledged young by laying the extra egg(s). These behaviours are referred to as 'insurance' and 'bet-hedging', but they do not involve any sacrifice of expected fitness. Thus, they are qualitatively different from the situations we will emphasize, where individuals actually suffer a *loss of expected or average* fitness in order to reduce the variance of fitness.

Bet-hedging is often associated with polymorphism, and all three of the literatures mentioned above contain statements to the effect that genetic or phenotypic variation is in some sense an *adaptive* response to environmental variation. But as Felsenstein (1976) says of the genetic literature, 'The reasoning behind [these statements] is no more subtle, no more convincing, than a feeling that genetic variation is necessary to give the population options in the face of environmental variation.' Arguments based on the assumption that evolution will maximize some parameter related to the population's long-term success often fail to hold up under close examination, and they

have steadily declined in frequency following Williams's (1966) critique of group selection. Yet some very successful explicit bet-hedging models were based (at first) on just this assumption. Perhaps the most famous of these is Cohen's (1966) model for the evolution of seed dormancy, which we discuss below.

Although bet-hedging arguments are most often used to explain genetic or phenotypic polymorphisms, they are also sometimes used to explain or predict apparent *reductions* of phenotypic variation. Where polymorphism is to be explained, the arguments can be likened to 'Don't put all your eggs ...', and where constancy is to be explained, they can be likened to 'A bird in the hand ...'. In the first case, the mechanism of bet-hedging is diversification or risk-spreading of a kind that usually *reduces* the variance of an *aggregate* outcome, while possibly *increasing* the variance of certain *individual* outcomes. In the second case, the mechanism is very different in that it involves risk-avoidance at the level of the individual.

At least five different definitions of 'bet-hedging' are in common use. We review these briefly before narrowing our focus to processes that involve a sacrifice of expected fitness.

2.1 FACULTATIVE DEVELOPMENTAL OR BEHAVIOURAL ADJUSTMENTS OF THE PHENOTYPE, IN RESPONSE TO THE CURRENT STATE OF THE ENVIRONMENT

The ideal response to environmental variation would clearly be to express the best possible phenotype for each contingency as it happened, or, if that were not possible, to choose phenotypes on the basis of cues that predicted future states of the environment. Such responses are sometimes referred to as bet-hedging, so we mention them here for the sake of completeness. They have little in common with the other processes we will discuss, except that they may evolve in response to environmental variation. We assume in most of what follows that the environment is truly unpredictable, in the sense that any options open to the individual must be exercised in ignorance of what the actual state of the environment will turn out to be.

2.2 ADJUSTMENT OF A PARAMETER TO MAXIMIZE FITNESS UNDER UNCERTAINTY

The clutch sizes of brood-reducing birds, discussed above, are a good example of this category, as are many other quantitative characters. For example, bones need to be strong enough to handle extreme stresses that may occur only once in a typical lifetime, but there is great uncertainty as to what the maximum stress will be. Resources put into bones cannot be put into, say, eggs. Finding the optimal bone thickness involves making a 'bet' on the distribution of stresses likely to be encountered by the individual. Bones are

overdesigned for average conditions. The 'extra' thickness can be called bet-hedging, but if it is adjusted to maximize *expected* fitness (as is usually assumed), then it is not bet-hedging in the stronger senses to be discussed below.

2.3 GENETIC POLYMORPHISM MAINTAINED BY SPATIAL OR TEMPORAL VARIATION OF THE ENVIRONMENT, OR BY FREQUENCY-DEPENDENT SELECTION

The evolutionary 'flexibility' given to a population by its genetic variation is sometimes viewed as bet-hedging at the population level, as was mentioned above (e.g. Tauber *et al.* 1986). Under frequency-dependent selection, an individual's relative rarity can be viewed as a kind of wager on the environmental uncertainty generated by the diversity of phenotypes it will encounter among members of its own species, as under definition (2.2). But the genetic polymorphism itself is not 'insurance' in the sense discussed at the outset; it does not exist *because* it increases the population's evolutionary 'options', and it does not reduce the variance of individual fitness. Indeed, under certain circumstances to be discussed below, the polymorphism may *increase* the variance of individual fitness, while reducing the variance of the population's mean fitness.

2.4 REDUCTION OF THE VARIANCE OF INDIVIDUAL FITNESS AT A COST TO EXPECTED FITNESS

This is bet-hedging of the 'bird in the hand' kind. It requires temporal environmental variation. Individuals sacrifice some expected fitness so as to reduce their uncertainty, or variance, of fitness. In the simplest models, the balance is struck so as to maximize the *geometric-mean* fitness, which is more sensitive to variance than is the arithmetic-mean fitness, as will be discussed further below. Verner's (1965) argument for reduction of the variance of progeny sex ratios is one of the first applications of the principle. Slatkin's (1974b) review of Gillespie's (1974a) model for the evolution of reduced variance of offspring numbers is entitled 'Hedging one's evolutionary bets', and may be the first publication to use the term with this intended meaning. Boyce and Perrins (1987) have recently argued that the apparently suboptimal clutch sizes of great tits are a variance-reduction strategy of essentially this kind.

2.5 PROBABILISTIC DIVERSIFICATION OF THE PHENOTYPES EXPRESSED BY A SINGLE GENOTYPE

This is bet-hedging of the 'Don't put all your eggs in one basket' kind. As in definition 2.4, it requires temporal variation of the environment, and is an instance of the geometric-mean principle. Expected fitness is reduced, but here the variance of realized individual fitnesses may actually be *increased*. None

the less, the geometric-mean *expected* fitness of individuals (averaged over the distribution of their alternative phenotypes—which is to say, over ‘baskets’) is maximized. Cohen’s (1966) model of seed dormancy is the first and best-known example. The principle has been discussed more generally by Cooper and Kaplan (1982), Kaplan and Cooper (1984), Walker (1986), and others.

We reserve the term ‘bet-hedging’ for definitions 2.4 and 2.5. This usage is a matter of taste, of course, but it serves to indicate that 2.4 and 2.5 differ fundamentally from the other definitions. Regardless of terminology, the distinction is an important one. Our account of the arguments and models will emphasize the following conclusions:

- (1) Genetic polymorphism can be maintained in large populations by a range of conditions involving either spatial or temporal variation in the environment (which is to say, in the relative fitnesses of particular genotypes).
- (2) Genuine bet-hedging can evolve only under population-wide temporal variation, which is a subset of the conditions potentially supporting genetic polymorphism.
- (3) Under these conditions, both bet-hedging and genetic polymorphism can be understood as consequences of the geometric-mean-fitness principle.
- (4) But a bet-hedging strategy must be realized as the variable (or sometimes, relatively constant) phenotypic expression of a *single* genotype, not as a genetic polymorphism; this is one of several respects in which a bet-hedging strategy differs from a mixed ESS, which can usually be realized as a genetic polymorphism.

3. Polymorphism in variable environments

3.1 SPATIAL VARIATION

Under this heading we discuss only the basic results for models of large populations with discrete, non-overlapping generations, since we are interested mainly in the selective forces induced by environmental variation. Although our conclusion will be that spatial variation does *not* give rise to bet-hedging, we discuss the spatial case anyway, because it provides an illuminating contrast to the temporal case, where bet-hedging does arise.

If different alleles at a locus are favoured in different environments, and if there is limited migration among the populations inhabiting those environments, then each local population receives a continual input of genes that are favoured (and therefore at high frequency) somewhere else. For a wide range of fitness differences and migration rates, this process can give rise to a stable genetic polymorphism within each population. Haldane (1930) was apparently the first to derive an explicit version of this model, which has been extended in many directions since then. (For entry to the very large literature, see Felsenstein 1976; Hedrick *et al.* 1976; Endler 1977; Walsh 1984; Christiansen 1985.)

As migration increases, genetic differentiation erodes, and in the limit of complete panmixia, each genotype’s fitness is simply its average over the various local environments, weighted by the frequencies of those environments. The fact that fitness is variable becomes irrelevant, and in the absence of heterozygote advantage, the allele with the highest average fitness goes to fixation. But Levene (1953) showed that there is one assumption under which polymorphism can be maintained in a purely spatial ‘multiple-niche’ model with completely free migration. In Levene’s model the density-dependent regulation of population size occurs *within* the various niches, not at the level of the global population. Thus, the number of adults contributed to the mating pool by each niche is independent of the average fitness of the individuals occupying that niche. In the simplest case, each of N niches receives $1/N$ of the zygotes, and sends back $1/N$ of the adults. The outgoing adults differ in gene frequency from the incoming zygotes, reflecting the pattern of selection within the particular niche, but the *number* of outgoing adults does not depend on their average fitness.

With two equally frequent niche types and two haploid genotypes, the condition for protected polymorphism can be stated as follows. If the fitness of one genotype is scaled to 1.0 in both niches, then the arithmetic-mean fitness of the other genotype must be greater than 1.0, but its harmonic mean must be less than 1.0. (The harmonic mean of N numbers is the reciprocal of the arithmetic mean of their reciprocals.) For example, if the fitness of the two genotypes are

	A_1	A_2
Niche 1	2	1
Niche 2	0.5	1

then the arithmetic-mean fitness of A_1 is 1.25, and its harmonic mean is $1/\{[(1/2) + (1/0.5)]/2\} = 0.8$. Thus, the condition for polymorphism is satisfied. In fact, A_1 and A_2 will be equally frequent at equilibrium. To see why, note that their fitnesses are in the ratio 2:1 within each niche, and recall that the key assumption of the Levene model is that each niche makes a fixed (and in this case equal) contribution to the global mating pool (Dempster 1955). Here each genotype has a net fitness advantage of 25 per cent when rare, so a population will converge rapidly to the equilibrium gene frequency.

Although the genotypic fitnesses within each niche are fixed in the Levene model, its scheme of locally density-dependent population regulation gives rise to a form of ‘soft selection’ in which frequency dependence appears at the level of the global population (Christiansen 1975, 1985; Karlin and Campbell 1981; Walsh 1984). A similar kind of induced frequency dependence often appears in models of sexual selection, even though the viabilities and female mating preferences may themselves be fixed (Christiansen 1985; Seger 1985b).

For the diploid version of Levene’s model, a sufficient condition for the

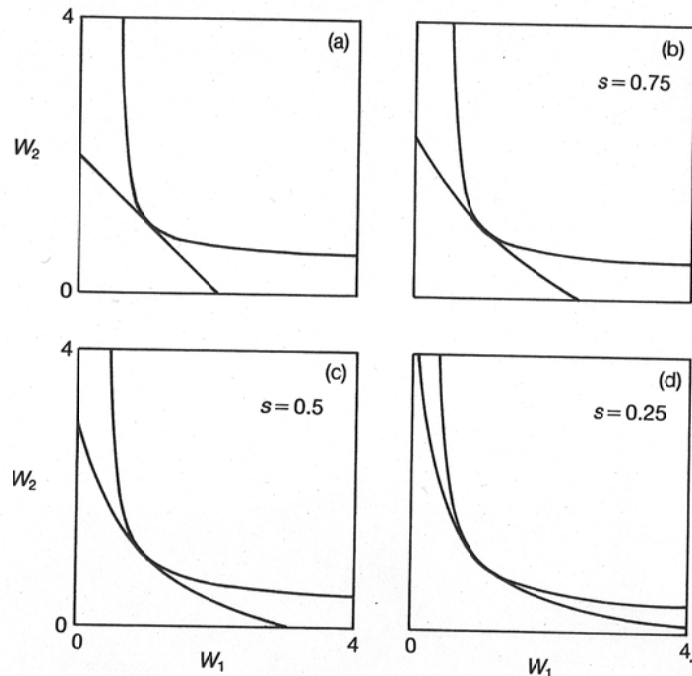


Fig. 1. Regions of protected polymorphism for haploid models of spatial and temporal environmental variation. (a) W_1 and W_2 are the fitnesses of allele A_1 in a two-niche Levene model, relative to the fitnesses of allele A_2 in the same two niches. The region between the curves corresponds to pairs of fitnesses for which there is protected polymorphism, given that the niches are of equal size. The inner curve is a straight line, corresponding to an arithmetic-mean fitness of unity. The outer curve converges not to the axes, but to the lines $W_1 = 0.5$ and $W_2 = 0.5$.

(b-d) W_1 and W_2 are the fitnesses of A_1 in two equally frequent kinds of years relative to the fitnesses of A_2 in those years, in a 'lottery' model with overlap of generations. s is the proportion of each year's breeding population that will survive to take part in the next breeding season, and $1 - s$ is therefore the proportion of each year's breeding population that consists of new recruits. As s approaches unity, the set of fitness pairs that give protected polymorphism converges on that for the corresponding spatial model (Fig. 1a). As s approaches zero, this set shrinks dramatically, and converges on the hyperbola $W_2 = 1/W_1$, which gives a geometric-mean fitness of unity under the assumptions of this model.

maintenance of polymorphism is that the harmonic-mean fitness of the heterozygote exceed that of either homozygote (harmonic-mean overdominance), but this condition is not necessary (Maynard Smith 1962, 1970; Prout 1968). For example, with complete dominance of one allele, the harmonic mean of one homozygote will equal that of the heterozygote, and the conditions for polymorphism are identical to those for two haploid genotypes (Fig. 1a). Because the harmonic mean is always less than or equal to the arithmetic mean, harmonic-mean overdominance can easily appear under arith-

metic additivity or even underdominance. But Maynard Smith and Hoekstra (1980) show that a given set of fitnesses will maintain polymorphism only over a narrow range of relative niche sizes, in the Levene model and several variants, unless the fitness differences are large.

Li (1955) and Cannings (1973) show that at equilibrium, the geometric-mean fitness of the niches is maximized. (The geometric mean of N numbers is the N th root of their product.) This is an intriguing result, but its ecological meaning is not obvious, since by assumption the patches have fixed productivities. Indeed, real populations probably seldom have *separate* density-dependent regulation and a *common* mating pool. Restricted dispersal, habitat selection, and assortative mating (possibly leading to speciation) can all be favoured under the ecological conditions represented by the Levene model (e.g. Maynard Smith 1962, 1966; Balkau and Feldman 1973; Gillespie 1981; Seger 1985a). But there is one common situation that fits Levene's model almost perfectly: the sexes.

The males and females of a bisexual species can be viewed as subpopulations that occupy distinct ecological environments. They begin each generation with the same genotype frequencies, and they always make equal genetic contributions to the next generation. The only difference from Levene's model is that the occupants of each 'niche' mate exclusively with occupants of the other. Owen (1953) was the first to show that genetic polymorphism can be maintained, without overdominance or explicit frequency dependence, if some genotypes are relatively fitter in males, while others are relatively fitter in females. Haldane (1962) and Li (1963) derived similar results, both apparently unaware of Owen's work and of each other's. The result has been extended in various directions by Bodmer (1965), Kidwell *et al.* (1977), Seger and Trivers (1986), and others. Of these papers, only the one by Kidwell *et al.* points out the relationship between the two-sex model and the two-niche Levene model, and few papers in the much larger literature on Levene's model refer to Owen's result, even though the structures of the two models and the conditions for polymorphism are very similar under diploidy, and identical under haploidy.

There is also a close relationship between the Levene model and the principle governing evolution of the sex ratio. At equilibrium under random mating there is equal investment in the two sexes (Fisher 1930). MacArthur (1965) pointed out that the product of the numbers of males and females alive at any age is maximized at this equilibrium, regardless of their relative costs or rates of survival. Thus, the geometric mean abundance of the sexes is also maximized. Levins and MacArthur (1966) cite Li (1955) in their paper on the Levene model, so MacArthur probably knew that selection maximizes the geometric-mean fitness of the niches, yet he apparently did not notice the connection between the Levene model and the sex-ratio model. A geometric mean is maximized in both models for essentially the same reason: the 'niches' make *fixed* (and in the case of the sexes, equal) genetic contributions to the

next generation. The sex-ratio product theorem has been generalized to cover a wide range of sex allocation problems (Charnov 1982, 1986a), but its relationship to Li's result still seems not to be widely appreciated.

Owen (1953) showed that there can be *two* stable polymorphic equilibria (with an unstable equilibrium lying between them) in the diploid two-sex analogue of Levene's model, if there is overdominance (heterozygote advantage) in one sex and underdominance in the other. Complicated patterns of alternative stable equilibria also appear in generalized spatial models with asymmetrical migration rates (e.g. Hedrick 1983).

Polymorphisms may easily arise under spatial variation, because simple patterns of selection, migration, and population regulation will generate frequency dependence at the level of the global population, *if* there is no general-purpose genotype that confers high fitness in all niches (e.g. Lively 1986). In effect, each allele 'specializes' on one niche, and it may do very poorly (it may even be lethal) in other niches. But at gene-frequency equilibrium, all alleles have in effect the same marginal fitness.

Even though genetic polymorphism can be maintained by purely spatial environmental variation, we see no way to interpret such polymorphism as evidence of bet-hedging, for the following reason. Consider a 'bet-hedging' genotype that produced, with the appropriate probabilities, the complete array of phenotypes present in the equilibrium mixture of genetically determined phenotypes. In a spatial model with complete mixing, this 'bet-hedging' phenotype would do no better than the equilibrium mixture of genetically determined phenotypes. In a model with restricted migration, such a mutant would actually do *worse* than the mixture, which would tend to differentiate in the various subpopulations. Indeed, migration tends to undermine local adaptation in any purely spatial model. Under the simple assumptions of these models, speciation would increase the average fitness of individuals and of populations. Then, in the absence of local heterozygote advantage or explicit frequency dependence, each newly isolated population would become monomorphic.

3.2 TEMPORAL VARIATION

Environments vary in time on scales that range from milliseconds to millions of years. Dempster (1955) showed that for temporal fluctuations on a scale of generations, the relevant measure of fitness is its geometric mean. Dempster's result is the starting-point for all subsequent models of genetic evolution in temporally varying environments. The haploid version for discrete non-overlapping generations is extremely simple and elegant.

Let the fitnesses of A_1 and A_2 in generation t be in the ratio $W_t:1$, and let their frequencies be p_t and $q_t = 1 - p_t$. Then the recurrence equation for the ratio of the gene frequencies is

$$p_{t+1}/q_{t+1} = (p_t/q_t)(W_t/1),$$

which gives

$$\begin{aligned} p_{t+2}/q_{t+2} &= (p_t/q_t)(W_t/1)(W_{t+1}/1) \\ &= (p_t/q_t)W_tW_{t+1}, \\ p_{t+3}/q_{t+3} &= (p_t/q_t)W_tW_{t+1}W_{t+2}, \end{aligned}$$

and so on. After any number of generations, the frequency of A_1 will have increased if the *product* of its fitnesses in those generations is greater than unity, and it will have decreased if the product is less than unity. This is equivalent to saying that the fate of A_1 depends on its geometric-mean fitness over the sequence of generations being considered. (Without loss of generality we scaled the fitnesses of A_1 to those of A_2 in the same generation, so that the arithmetic- and geometric-mean fitness of A_2 is always unity.)

The geometric mean is the natural measure of long-term fitness under temporal variation because, like population growth itself, it is inherently multiplicative rather than additive. It is therefore very sensitive to occasional small values, and must be zero for any sequence that includes even a single value of zero. If there is any variation, the geometric mean will be less than the arithmetic mean. The logarithm of the geometric mean is the arithmetic mean of the logarithms of the individual values, so the geometric mean becomes additive on a logarithmic scale of measurement. Thus, the genotype with the highest geometric-mean fitness will also have the highest *arithmetic-mean log* fitness.

Given a fixed distribution of relative fitnesses, one or the other allele always goes to fixation in this simplest purely temporal model. In this respect, temporal variation is qualitatively different from spatial variation, which can maintain protected polymorphism in the simplest of models. But under diploidy, temporal variation can maintain polymorphism without overdominance or frequency dependence. Haldane and Jayakar (1963) considered the case of complete dominance, and showed that polymorphism will be maintained if the arithmetic-mean fitness of the recessive homozygote is greater than that of the other two genotypes, while its geometric-mean fitness is lower. In general, the condition for protected polymorphism is that the *geometric-mean* fitness of the heterozygote exceed that of either homozygote (Gillespie 1973; Hartl and Cook 1973; Karlin and Liberman 1974), which can easily hold even where the expected (arithmetic-mean) fitnesses of all genotypes are equal. Because selection is constantly changing direction, the equilibrium is best described as a probability distribution of gene frequencies (see Hartl and Cook 1976 for some examples).

Although the genotype with the highest geometric-mean fitness is favoured (and certainly goes to fixation in the haploid case), the *population's* geometric-mean fitness is not necessarily maximized at equilibrium, even discounting the fluctuations of gene frequency that are induced by the environmental fluctuations. This can easily be seen in a simple numerical example

that will also introduce the two main kinds of bet-hedging that are supported by temporal variation.

Consider a haploid annual population that encounters 'wet' and 'dry' years with equal frequency, and let there be four different genotypes with the following fitnesses in the two kinds of years.

	A ₁	A ₂	A ₃	A ₄	
Wet	1	0.6	0.785	0.776	(1, 0.6)
Dry	0.58	1	0.785	0.815	(0.58, 1)
Arithmetic mean	0.79	0.8	0.785	0.796	
Geometric mean	0.762	0.775	0.785	0.795	

Suppose that the population is initially fixed for allele A₁ (the wet-year specialist), and that A₂ (the dry-year specialist) has just appeared as a rare mutant. Because A₂ has the higher geometric-mean fitness, it will increase to fixation, and the population's geometric-mean fitness will of course be raised as a consequence. However, it is *not* true that the population's geometric-mean fitness is *maximized* by the fixation of A₂. Because each of the genotypes is fitter than the other in one kind of year, the year-to-year variance of the population's mean fitness will be lowest at some intermediate frequency of A₂. This suggests that the population's geometric-mean fitness might be maximized at an intermediate frequency and in fact when A₁ has declined to a frequency of 0.44, the population's geometric-mean fitness reaches its maximum of 0.795, and thereafter declines as A₂ works its way to fixation.

Now suppose that A₂ is fixed, and A₃ (the jack-of-all-trades allele) is introduced as a rare mutant. A₃ is equally undistinguished in both kinds of years, and is actually worse than either A₁ or A₂ on average. But because its fitness does not vary, it has a higher geometric-mean fitness than does A₂, and it therefore increases to fixation. This time the population's arithmetic-mean fitness is lowered as a consequence. But as before, its highest geometric-mean fitness occurs at an intermediate gene frequency, even though this time the population's fitness *variance* will clearly be lowest (zero) when A₃ has gone all the way to fixation.

Finally, with A₃ fixed, introduce A₄ (the phenotypically polymorphic allele) as a rare mutant. Forty-four per cent of the time A₄ develops the phenotype of A₁ (the wet-year specialist), and 56 per cent of the time it develops the phenotype of A₂ (the dry-year specialist). This gives it an average fitness in wet years of 0.776, and an average in dry years of 0.815, for a geometric mean of 0.795. Thus, A₄ drives A₃ to extinction. At fixation for A₄, the population once again has year-to-year variance in mean fitness. In fact, it looks exactly like the unstable mixture of A₁ and A₂ that produced the highest population geometric-mean fitness. Yet neither A₁ nor A₂ (nor both) would survive for long against A₄, because their *individual* geometric-mean fitnesses are lower! One year out of two, each suffers the full cost of being

maladapted, while *some* A₄ individuals do well *every* year (and only some do poorly).

Allele A₄ employs the sophisticated bet-hedging strategy that has been called 'adaptive coin-flipping' (Cooper and Kaplan 1982; Kaplan and Cooper 1984) and 'stochastic polyphenism' (Walker 1986). This kind of bet-hedging corresponds to our definition 2.5 above. The idea traces back to Levins's (1962, 1968) model of 'fitness sets' and 'adaptive functions'. The fitness set described by the table above is concave; both specialist alleles (A₁ and A₂) are fitter, on average, than the generalist (A₃). Under temporal variation, the adaptive function is the population's geometric mean fitness. Levins's analysis shows that under these circumstances, 'the optimal population is polymorphic, a mixture of types optimally adapted to the two niches occurring in proportions that vary with [the frequencies of the two temporal niches]' (Levins 1962).

Levins assumed that the optimal polymorphic population will tend to evolve. But if the polymorphism must be genetically determined, then it is likely to be unstable and an inferior generalist such as A₃ may displace even the best specialist (see Schaffer 1974). But if the polymorphism can be produced by *one* genotype (such as A₄) that in effect plays developmental roulette, then the 'optimum' for individuals may coincide with that for the population as a whole, under the constraints described by the fitness set.

The form of bet-hedging practised by A₄ is 'risk-spreading' of the kind advocated in 'Don't put all your eggs in one basket'. Some baskets come through safely, and some hit the floor. It should be emphasized that those A₄ individuals who happen to develop as 'wets' (imitating A₁) have lower arithmetic- and geometric-mean fitnesses than do those who happen to develop as 'drys' (imitating A₂). This is what distinguishes genuine risk-spreading from a mere polymorphism maintained by frequency-dependent selection; some of the equilibrium phenotypes may be truly worse than others, by almost any standard.

Allele A₃ is also a genuine bet-hedger, even though it is less interesting than A₄ and competitively inferior. In effect, A₃ plays a conservative 'bird in the hand' strategy, corresponding to our definition 2.4. It reduces its *variance* of individual fitness (over environments), at a cost to its *expected* fitness. A₃ is jack of all trades and master of none, but under temporal environmental variation it can none the less displace a mixture of masters (A₁ and A₂). The low-variance phenotype of A₃ might result from developmental 'buffering' or 'homeostasis' of the classical kind, but alternatively, it might result from a facultative plasticity that allowed individuals to respond appropriately to the current state of the environment (e.g. Levins 1963; Stearns 1982; Caswell 1983; Orzack 1985; Via and Lande 1985). This may seem to contradict what we said earlier, under definition 2.1, about facultative adjustments of the phenotype, but in fact it does not. Bet-hedging takes place on the *fitness* scale; specifically, it involves a trade-off between the mean and variance of fitness. If

the ability to make facultative adjustments of the phenotype is costly, then a facultative phenotype might well be the realization of a bet-hedging strategy, but it need not be. In either case, the phenotypic adjustments themselves are expected to maximize immediate expected fitness under the given constraints.

Although the simple haploid temporal models with non-overlapping generations will not maintain protected genetic polymorphisms, the equivalent models with *overlapping* generations and iteroparity will readily do so. The easiest way to introduce iteroparity is to let a proportion, s , of this year's adults survive (independent of their ages and genotypes) to breed again next year in an adult population of the same total size. Thus, each year's adult population consists of s veterans and $(1 - s)$ new recruits; the latter are taken at random from the previous year's offspring. This population structure is often referred to as the 'lottery model' (Chesson and Warner 1981), because each year a fixed number of juveniles win places in the adult population, regardless of the size of the juvenile cohort.

If we again consider a haploid population with two genotypes A_1 and A_2 , and if we scale the fitnesses in each generation to those of A_2 , then the recurrence equation for the frequency of A_1 is

$$p_{t+1} = p_t \{s + (1 - s)W_t/V_t\},$$

where W_t is the relative fitness (net offspring production) of A_1 in generation t , and $V_t = 1 + p_t(W_t - 1)$ is the population mean fitness. When $s = 0$, there is no adult survival, and the model reduces to Dempster's model of non-overlapping generations. But as s increases, the temporal fluctuations tend to average out within the lifetime of a single individual, and protected polymorphisms are maintained for increasingly broad distributions of W (Figs. 1b-d). In the limit as s approaches unity, the model becomes a temporal analogue of Levene's spatial model (with individual lifetimes playing the role of space), and the conditions for maintenance of polymorphism converge on those of the Levene model (Fig. 1a).

Selection tends to maximize the geometric-mean fitness of the niches in Levene's model, as was mentioned earlier. Here, selection tends to maximize a weighted sum of the geometric-mean *population* and *individual* fitnesses. For the simplest model with two kinds of years in equal proportions, as described above, the mean gene frequency is (to a good approximation) that which maximizes

$$f(P) = s\{V_1(P)V_2(P)\}^{0.5} + (1 - s)\{P(W_1W_2)^{0.5} + (1 - P)\},$$

where P is the expected frequency of A_1 , and the $V_i(P)$ and W_i are the population and individual fitnesses, respectively, in the two kinds of years. With low adult survival (s near zero), the population's average composition will tend to emphasize individual geometric-mean fitness. But as s increases, more weight is given to the population geometric mean, which will often be maximized by polymorphism.

Although genetic polymorphisms can be maintained with $s > 0$ in this iteroparous version of the basic temporal model, such polymorphisms are vulnerable to invasion by diversifying bet-hedgers like the allele A_4 . If such an allele produces a phenotype that perfectly imitates the established genetic polymorphism, its spread will clearly not affect the *population's* geometric-mean fitness, which appears in the first term of the expression above. But such an allele *can* increase the average *individual* geometric mean. Thus, through its effect on the second term of the expression, the spread of such a polymorphic bet-hedging genotype can increase the composite fitness function f . The *size* of the advantage that can be derived from bet-hedging declines as s increases, and this is clearly reflected in the functional form of f , because s is the weight applied to the *population's* geometric-mean fitness, which is not changed by the spread of the bet-hedging allele. Thus, to the extent that phenotypically polymorphic bet-hedging strategies are relatively costly to develop, we might expect bet-hedging to be more common (and genetic polymorphisms less common) among relatively short-lived species, other things being equal.

3.3 COMBINED SPATIAL AND TEMPORAL VARIATION

Real environments vary both spatially and temporally, of course, so realism would seem to demand models that combine both kinds of variation. Unfortunately, such models tend to be complex and very difficult to analyse. Levins (1962, 1968) applied his method of fitness sets to the case of a geographically unstructured (i.e. Levene) population in which the relative proportions of two niches vary from year to year. He concluded that the outcomes would tend to be more or less like those for pure spatial or pure temporal variation, depending on which form of variation was more important.

Gillespie (1974b, 1975, 1981) has analysed a series of explicit haploid models with arbitrary migration rates and temporal variation within sub-populations. Higher migration rates make polymorphism more likely. This is what we might expect, because migration increases the extent to which each genotype experiences the variation as spatial rather than temporal, and thus makes the model more 'Levene-like'. If the migration rate itself is allowed to evolve, it tends to decrease 'when there is, in some sense, more spatial than temporal variation', and it tends to increase when there is more temporal than spatial variation (Gillespie 1981). In the latter case, it seems likely that migration could be interpreted as a genuine bet-hedging strategy, since a genotype that distributes itself over the available *environments* (by migrating) will average its fitnesses in much the same way as one that distributes itself over the available *phenotypes* (by diversifying). Whether migration increases or decreases, the quantity that tends to be maximized is the population's geometric-mean fitness (Gillespie 1981). This is gratifying, given Li's (1955) and Dempster's (1955) results for the elementary component models.

No one seems yet to have tackled an explicit genetic model with spatio-temporal variation, restricted migration, and iteroparity, but Chesson (1985), and Comins and Noble (1985) have studied population-dynamic 'lottery' models of species' interactions in 'uniformly variable' environments where each patch has the same distribution of states. Both sets of authors point out that the models are open to reinterpretation as haploid genetic models for single species. Where the species involved are long-lived and highly iteroparous, spatial and temporal variation both promote coexistence (or in the genetic interpretation, polymorphism), and in combination their effects are roughly additive. But for short-lived organisms with few reproductive episodes, spatial variation is much more effective at promoting coexistence than is temporal variation, as the genetic models would lead us to expect.

4. Species coexistence in variable environments

Environmental variation has traditionally been viewed as a destabilizing force that tends to simplify ecological communities (e.g. May 1973); yet, disturbance has also been viewed as the creator of successional niches for 'colonists', 'fugitives', and 'tramps' (e.g. Slatkin 1974a; Diamond 1975; Horn 1975; Leigh 1975). The idea that migration allows species to persist in the face of spatio-temporal variations of the environment has frequently been expressed in the language of bet-hedging. For example, the discussion section of May's (1973) paper on community stability under temporal variation begins with the comment that

There are, as pointed out by Levins (1969, 1970), den Boer (1968), MacArthur and Wilson (1967), Smith (1972), Maynard Smith (personal communication), Roff (1974), and others, many circumstances where the interplay between migration and extinction in a number of local populations in a spatially heterogeneous environment can have an important stabilizing effect of the 'not putting all eggs in one basket' kind.

More recently, various forms of the argument that risk-spreading favours persistence in a variable environment have been advanced by Hubbell (1979), den Boer (1981), Stearns and Crandall (1981), Andrewartha and Birch (1984), and others (for recent reviews see Chesson and Case 1986; Strong 1986; Hubbell and Foster 1986). Central to most of these arguments is the idea that long-lived or widely dispersing species may have very long average times to extinction in environments that vary both spatially and temporally, such that communities could sustain high levels of standing diversity, far above what might be considered their deterministic equilibria, given modest inputs of new species through immigration and speciation. On this view of community dynamics, an important evolutionary question is whether natural selection will actually tend to favour the kinds of life-history traits that promote long-term persistence on an overcrowded, constantly heaving adaptive landscape (e.g.

Stearns and Crandall 1981). At least to a limited extent, life-history theory seems to answer in the affirmative (see below).

A somewhat stronger view of the possible role of environmental variation in supporting species diversity emerges from Levins's (1979) model of resource utilization, in which the variance (and other higher statistical moments) of resource abundance may constitute what amount to distinct resources, each of which might support a species specialized to exploit (and thereby reduce) it. In Levins's unforgettable metaphor, two species can exist on one varying resource if one species 'eats the variance'.

Felsenstein's (1979) 'completely chaotic' model of r - and K -selection may be a concrete realization of this idea. The model has discrete, non-overlapping generations and no spatial structure. Two haploid morphs are subject to a very strong (literally kinky) form of density-dependent selection that gives rise to chaotic fluctuations of their absolute and relative abundances. Felsenstein refers to the morphs as 'genotypes', but they are open to interpretation as species. He finds that protected polymorphisms may exist if the morph that has what amounts to the higher r also has what amounts to the lower K . In other words, if densities (and thus, implicitly, resources) are continually fluctuating, there may be room for one morph that is relatively good at exploiting superabundance and another that is relatively good at enduring scarcity. Felsenstein states that polymorphism can also be maintained in a haploid version of Roughgarden's (1971) model of r - and K -selection, where densities are periodically lowered by extrinsic seasonal effects, and he points out that, in both models, the mechanism favouring polymorphism is frequency dependence of the relative fitnesses, which is induced by the scheme of density-dependent population regulation.

The lottery model of Chesson and Warner (1981; also see Sale 1977, 1978; Warner and Chesson 1985) is also very much in the spirit of Levins's (1979) model, in that an abstractly defined form of temporal environmental variation (which could be thought of as resource variation) favours coexistence under conditions that would otherwise not permit it. In this model the frequency dependence is generated by iteroparity combined with competition for a fixed total number of positions in the juvenile-recruitment lottery, as explained above, where we interpreted the model to represent the population genetics of a single haploid species. There, we also pointed out that a stable mixture of true-breeding morphs could be replaced by a single bet-hedging form that developed as one or the other of the two morphs, with the appropriate probabilities. The same strategy would work at the level of species under the community-dynamics interpretation of the model.

This suggests, by analogy with the genetic interpretation, that species diversity can be maintained by purely temporal environmental variation only to the extent that species are actually *unable* to practice phenotypically diversified bet-hedging (definition 2.5); otherwise, a generic Tropical Tree that imitated whole communities might take over vast areas of the world. None

the less, given unavoidable constraints on the phenotypic plasticities of individual species, the patterns of longevity, iteroparity, and dispersal that promote coexistence may themselves be life-history traits that evolved in part because they allowed individuals to hedge their reproductive bets. As noted by Real (1980), the resulting diversity is merely a 'by-product' of adaptation (and of its limits).

5. Life-history evolution in variable environments

Models of life-history evolution typically focus on trade-offs involving growth, maintenance, and reproduction. The classic problem is to understand when selection favours semelparous or iteroparous reproduction (e.g. Cole 1954; Gadgil and Bossert 1970; Charnov and Schaffer 1973). Iteroparity can be favoured under many sorts of conditions, and in particular, under temporal variation of the environment (e.g. Murphy 1968; Schaffer and Gadgil 1975; Hastings and Caswell 1979; Bulmer 1985; Charnov 1986b), especially if juvenile survival is more strongly variable than adult survival. Part of the reason for this is that geometric-mean fitness will usually be increased by averaging several random reproductive outcomes, if the variation is caused mainly by temporal environmental fluctuations. But if adult survival is more variable than juvenile survival, then semelparity may be favoured (Schaffer and Gadgil 1975; Bulmer 1985).

There is a sense in which *both* outcomes are seen in Cohen's (1966, 1968) model for the evolution of seed dormancy. In its simplest form, Cohen's model asks what proportion x of an annual plant's seed production should germinate next year, if with probability P the year will turn out to be good for growth and reproduction (in which case the average number of seeds produced per germinated seedling is S), and with probability $1 - P$ the year will be a disaster in which no plants set seed. The ungerminated seeds ($1 - x$) are assumed to remain in the soil, where a proportion D decay; the surviving members of the 'seed bank' ($(1 - D)$) germinate the following year with probability x , and so on.

A genotype that germinated completely ($x = 1$) would be eliminated in the first bad year, and a genotype with zero germination would be eliminated at once, so there must be an intermediate optimum. This is found by maximizing the geometric-mean rate of increase of a genotype employing germination strategy x , which is

$$V(x) = \{(1 - x)(1 - D) + xS\}^P \{(1 - x)(1 - D)\}^{1-P}.$$

Differentiating, equating to zero, and solving for x gives

$$x = (PS + D - 1)/(S + D - 1),$$

which is always close to P if S (the average number of seeds set in a good year) is a reasonably large number. Thus, the proportion of seeds that should

germinate is approximately equal to the probability that the year will be a good one. This version of the model is often described as applying to a population of asexual clones (or obligate selfers), but it also works for outcrossing hermaphrodites if we assume that each plant pollinates an average of S seeds raised by other plants.

There is no frequency dependence in this simplest version of the model, so it will not support a haploid genetic polymorphism. In effect, Cohen's model is Dempster's (1955) haploid temporal model with the fitnesses derived from a concrete biological scenario motivated by the germination behaviour of desert annuals. Partial germination is a pure bet-hedging strategy under the assumptions of Cohen's model. As Bulmer (1985) emphasizes, the strategy will work only if produced by 'a single genotype with variable germination behaviour'; the strategy cannot be realized as a genetic polymorphism. This expectation appears to be satisfied, at least qualitatively, for most annual species with partial germination (Palmbled 1969; Venable and Lawlor 1980; Ellner and Shmida 1981; Freas and Kemp 1983; Silvertown 1984, 1985; Ellner 1985a; Venable 1985; Venable *et al.* 1987). A low level of heritable variation might be expected, if neighbouring populations that exchange migrants have different optimum germination fractions, but high heritability of the germination fraction would not be consistent with the basic version of Cohen's model.

Seed-bank annuals achieve a kind of iteroparity through the sequential partial germination of a single cohort of seeds, and this would seem to be in keeping with the general results mentioned above. Adults are semelparous because their survival rates respond more strongly to environmental fluctuations than do those of their offspring (seeds). But if the world is looked at from the seeds' point of view, then 'iteroparity' makes sense, because *their* survival is less variable than that of their 'offspring' (adult plants).

Cohen's model has been extended in many directions. For example, Cohen (1967) and Venable and Lawlor (1980) allow the germination fraction to vary in response to cues that are correlated with the quality of the coming year. Templeton and Levin (1979) and Brown and Venable (1986) allow seed-set to vary in different kinds of years. Venable and Lawlor (1980) and Bulmer (1984) add spatio-temporal environmental variation and migration to the model. Ritland (1983) considers the interaction between seed dormancy and flowering time in an environment where both may be subject to bet-hedging.

Bulmer (1984) and Ellner (1985a,b) add density-dependent selection acting on the plants that germinate in a given year. In one of Bulmer's models, the density dependence can give rise to cyclical or chaotic fluctuations of density, even in a constant environment; the temporal variation of fitness caused by these density fluctuations selects for delayed germination, just as if the variance had been caused by the physical environment. Bulmer and Ellner both find that density dependence can affect the model's behaviour in important ways, as we might expect, because it almost always induces frequency dependence of the fitnesses of different phenotypes. Leon (1985) considers the

timing of germination within a season both as a response to extrinsic environmental uncertainty and as a response to competition among seedlings. In the latter case the best strategy becomes in part a frequency-dependent ESS, as it is in the density-dependent models of Bulmer and Ellner.

Insects living in unpredictable seasonal environments often face a diapause problem that is similar in many ways to the seed-dormancy problem. Animals enter diapause to avoid unfavourable conditions such as freezing or desiccation. For example, suppose that all adults will be killed by the first hard frost of the autumn, but that the day on which this will happen is highly uncertain. Then a larva produced in the middle of the season may in some years have plenty of time to complete development, emerge, and reproduce, but in other years it may find its life cut short, so that it would have done better to stay in the cocoon and emerge the following spring. If we simplify the model by making the outcomes 'all or nothing', with probabilities P and $1 - P$, as in the simple version of Cohen's model above, then the argument goes through almost exactly as before, and the best emergence probability turns out to be

$$x = (PS - 2)/(S - 2).$$

Here P is the probability that a direct-developing (non-diapausing) individual will succeed in producing a complete progeny, which consists of S offspring, and x is the probability that an individual develops directly and emerges (that is, does *not* enter diapause). We assume that the overwintering mortality rate D would be the same for the larva making the decision of whether to emerge as it would be for the larva's offspring (should the larva decide to emerge and reproduce); under this assumption there is no survival penalty for waiting, and so D cancels out. But there is a penalty of sorts for reproducing sexually (because insects are not hermaphroditic), and so the larva must expect to produce at least *two* offspring before the season ends (rather than one) if its probability of emerging is to be greater than zero.

The argument applies at any point in the season, given that some offspring are being produced at that time. As the season progresses, the probability of success following emergence (P) will decline, and so, therefore, will the probability of emergence (x). Note that P should actually be interpreted as the *relative* probability of success following emergence at this point in this season (as compared to the probability of success following emergence at the beginning of next season). This is not the same as the *absolute* probability of success, which might be fairly low even at the best times of year.

The model makes two striking predictions. First, there should not be a sudden switch between the production of emerging and diapausing offspring, but instead a gradual shift in the proportions of the two kinds. This is in sharp contrast to the results obtained by maximizing the average population growth rate, or where the environment is predictable, in which cases the optimal diapause fraction usually changes suddenly from zero to one (e.g. Cohen

1970; Taylor 1980, 1986a,b). Secondly, the first few diapausing offspring should appear as soon as P drops below unity, which could be early in the season. Many species of insects show partial diapause at certain times of the year (e.g. Tauber *et al.* 1986), and the proportion diapausing often varies with latitude (e.g. Denno and Dingle 1981; Tauber and Tauber 1982; Brown and Hodek 1983) or with other correlates of temporal environmental uncertainty (e.g. Dingle and Baldwin 1983).

The progenies of individual female pitcher-plant mosquitoes (*Wyeomyia smithii*) in New York show intermediate diapause fractions from early June through late August (Istock 1981). Istock explicitly attributes this pattern to bet-hedging. He observes that 'a bog may nearly dry up in midsummer', and that the weather may be 'highly unpredictable' early and late in the season. Istock also presents evidence of heritable genetic variation (among and within populations) in the probability of entering diapause under standardized laboratory conditions, and he interprets this variation as part of the bet-hedging strategy. Similar evidence has been found in other groups, including milkweed bugs and lace bugs (Dingle 1981; Tallamy and Denno 1981; Tauber *et al.* 1986). For reasons discussed above, we find it difficult to interpret these genetic polymorphisms *within* populations as elements of an adaptive bet-hedging strategy. Such polymorphisms could easily result from (i) gene flow among differently adapted populations, (ii) directional selection caused by historically recent changes in the distributions of key environmental variables, (iii) frequency-dependent selection, possibly arising from density dependence at various points in the season, or (iv) pleiotropic effects of genes under selection for some function other than diapause as such.

The organ-pipe mud-dauber *Trypoxylon politum* (a solitary sphecoid wasp) overwinters as a larva in its cocoon, pupating and emerging as an adult the following spring. In northern Florida there are two generations per year, but a few diapausing offspring are produced in the earliest days of the season, and a few direct-developing offspring are produced near the end (Table 1). A population studied by one of us (H.J.B.) produced offspring over a span of 21 weeks, from early May through late September. All eggs laid in week 1 developed directly into adults that emerged about 7 weeks later, but 10 per cent of the eggs laid in week 2 entered diapause. The proportion entering diapause increased steadily thereafter, but did not reach 100 per cent until week 14 (early August). In more northerly populations (North Carolina, Virginia, and New Jersey), larger fractions of larvae collected in late June entered diapause (72, 91, and 100 per cent, as compared with 47 per cent in Florida). These are the patterns to be expected under the assumptions of the simple model described above, if conditions sometimes deteriorate badly in mid-season, ruining the reproductive prospects of the direct-developing offspring.

It is not plausible to imagine that early diapause in Florida is maintained by the risk of a killing freeze in July or August. But it is not hard to find other factors that could act in much the same way. For example, there are many

Table 1
The proportion of *Trypoxylon politum* larvae entering diapause at different times of the season.

3-week interval	N	P
3 May–23 May	50	0.10
24 May–13 June	108	0.38
14 June–4 July	78	0.69
5 July–25 July	83	0.88
26 July–15 August	291	1.00
16 August–5 September	114	1.00
6 September–26 September	14	1.00

All larvae were produced in 1982. *N* is the total number that emerged in 1982 and 1983 combined (i.e. the total number collected minus the number that subsequently died). *P* is the proportion of all the viable larvae that entered diapause (i.e. the proportion of *N* that emerged in 1983). Mortality averaged about 30 per cent, and showed no trend over the season. (Unpublished data of H.J.B.)

species of parasites that attack larvae while the nest is still being provisioned (e.g. sarcophagid and bombyliid flies). An unusually high density of such parasites could virtually ruin the reproductive prospects of females that attempted to rear young late in the season. There could also be frequency-dependent competition for prey (spiders). If this tended to become more intense as the season progressed (and the wasp population increased) it could favour early diapause for reasons that had nothing to do with bet-hedging, although it is hard to see why the probability of entering diapause should increase so gradually, with such an early beginning, if this were the sole cause.

Alternatively, there may be conditions under which diapausing wasps are less successful than direct developers even relatively late in the season. For example, mud nests are highly vulnerable to damage from wind, flooding, or unusually hard rains. It is possible that in a major hurricane, almost the only survivors would be those wasps that had emerged shortly before the storm, since as mobile adults they could seek adequate shelter. In this case, emergence relatively late in the season could be a hedge against the risk of massive larval or pupal mortality, in just the same way that early diapause was a hedge against the risk of massive adult mortality.

The diapause model derived above assumes that all overwintering larvae emerge at the beginning of the next season, as seems to be true for most species. But small numbers of offspring may diapause for two winters or more in some species of Lepidoptera (Powell 1974; Shapiro 1979), Diptera (Sunose 1978), solitary Hymenoptera (MacSwain 1958; Krombein 1967; Parker 1980, 1984; Torchio and Tepedino 1982), and other insects (Danks 1983; Tauber *et al.* 1986). A few of these observations may be artefacts of laboratory rearing

conditions, but the behaviour is precisely what would be expected if entire years are occasionally unsuitable for reproduction.

6. Conclusions

In principle, the seed-dormancy and insect-diapause models can be tested quantitatively, because they involve dependent and independent variables that can be measured directly, and that vary over wide ranges. Not all bet-hedging models have these features. For example, Gillespie (1974a, 1977) shows that in finite populations, natural selection will favour a reduction in the variance of offspring numbers. This is a straightforward consequence of the geometric-mean principle, as is Verner's (1965) demonstration that a rigidly controlled sex ratio will be favoured in a finite population. Both arguments apply almost universally, and both simply say 'less variance is better', without making specific predictions as to how large the variance ought to be. In the case of Verner's argument for sex-ratio homeostasis, there is a plausible null hypothesis (the binomial distribution), but it is not obvious how a reduced variance of offspring numbers might be recognized. Similar problems beset any model that requires the direct measurement of small differences in fitness (e.g. Lewontin 1974, 1985). Migration may often be in part the realization of a bet-hedging strategy (e.g. Levin *et al.* 1984). But to disentangle bet-hedging from all the other functions served by migration might well prove impossible, leaving aside the difficulty of accurately measuring migration and its consequences.

Germination and diapause behaviours may be complex, but they and their quantitative genetics can be studied in detail. The critical independent variables, such as weather patterns, can also be measured, as can their average effects on reproduction. Just as important, the selective advantages associated with variable germination and diapause tend to be large, so that some form of the behaviour may be expected under a wide range of environments (roughly, whenever at least a few years or seasons occur in which the average reproduction falls short of replacement). By contrast, the selective advantage of sex-ratio homeostasis is very small in all but the smallest populations, and this may be part of the reason why few species of vertebrates seem to practise it (Williams 1979).

Bet-hedging strategies, based on risk-spreading can appear to be contrary to the best interests of the individuals playing them, and this is sometimes taken to mean that such strategies are maintained by group selection or require parental manipulation (e.g. Westoby 1981). Indeed, Cohen (1966) derived the seed-dormancy model by maximizing a population growth rate. This procedure gives the right answer for seed dormancy, because there is no frequency dependence, and because the germination polymorphism can be produced by a single genotype with variable expression. The same optimal germination fraction is obtained from a genetic model that vests control in

either the mother or the seeds. In the insect-diapause model above, we vested control in the larva. But maximizing a population growth rate would *not* give the right answer for the sex ratio, where population growth would usually be maximized by producing strongly female-biased progenies. The equilibrium sex ratio is a mixed ESS (Maynard Smith 1982), not a bet-hedging strategy. In general, all phenotypes have the same expected fitness at equilibrium in an ESS, but not in a bet-hedging strategy. Thus, an ESS can often be realized as a genetic polymorphism, but a bet-hedging strategy cannot. None the less, both can be maintained by ordinary natural selection acting at the level of individuals.

Under circumstances involving temporal variation of fitnesses, polymorphisms maintained by frequency dependence may provide opportunities for bet-hedging. An abstract example was given above, in the section on genetic models, and Verner's (1965) model of sex-ratio homeostasis in small populations is another. In a large population it may not matter whether the equilibrium sex ratio is realized as a genetic polymorphism or as a purely phenotypic polymorphism, because the equilibrium is neutral to the introduction of rare variants (e.g. Karlin and Lessard 1986). But the sampling error caused by small population size induces temporal fluctuations in the average fitnesses of males and females, and these fluctuations give a geometric-mean fitness advantage to the strategy of individually unbiased production of the sexes. Sex chromosomes provide one simple way to implement this strategy, since in principle they equalize the probabilities that any given offspring will be male or female. Verner's model shows that unvarying (rather than probabilistic) equalization of progeny sex ratios would be even *better* than a randomizing mechanism such as sex chromosomes. Thus, even though the sex polymorphism itself is an ESS maintained by frequency-dependent selection, particular sex-ratio strategies may employ bet-hedging tactics that exploit certain properties of the ESS. This kind of interplay between frequency dependence and bet-hedging seems likely to arise in other situations where the phenotypes involved in a polymorphism experience temporal variation of their relative fitnesses.

Sexual reproduction is one obvious candidate. It appears to be contrary to the immediate interests of individuals (e.g. Williams 1975; Maynard Smith 1978), and there are many arguments to the effect that it is a risk-spreading strategy maintained by environmental variation that is at least partly temporal (e.g. Hamilton 1982; Bell 1985). This would strongly imply bet-hedging, except that sex and recombination absolutely *require* genetic polymorphism, and the polymorphism is usually assumed to be maintained by frequency-dependent interactions with other species, such as parasites. But sex and recombination do not maintain the polymorphism; they merely exploit it as a means of creating phenotypic diversity, so they might well constitute a genuine bet-hedging strategy. Williams's (1975) 'lottery' metaphor speaks directly to this idea.

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References

- Andrewartha, H. G., and Birch, L. C. (1984). *The Ecological Web*. University of Chicago Press, Chicago.
- Balkau, B. J., and Feldman, M. W. (1973). Selection for migration modification. *Genetics*, **74**, 171-4.
- Bell, G. (1985). Two theories of sex and variation. *Experientia*, **41**, 1235-45.
- Bodmer, W. F. (1965). Differential fertility in population genetics models. *Genetics*, **51**, 411-24.
- Boyce, M. S., and Perrins, C. M. (1987). Optimizing Great Tit clutch size in a fluctuating environment. *Ecology*, **68**, 142-53.
- Brown, J. S., and Venable, D. L. (1986). Evolutionary ecology of seed-bank annuals in temporally varying environments. *Am. Naturalist*, **127**, 31-47.
- Brown, V. K., and Hodek, I. (eds.) (1983). *Diapause and Life Cycle Strategies in Insects*. Junk Publishers, The Hague.
- Bulmer, M. G. (1984). Delayed germination of seeds: Cohen's model revisited. *Theoret. Pop. Biol.* **26**, 367-77.
- (1985). Selection for iteroparity in a variable environment. *Am. Naturalist*, **126**, 63-71.
- Cannings, C. (1973). An increasing fitness function for a population with many niches. *Nature*, **241**, 47.
- Caswell, H. (1983). Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. *Am. Zool.* **23**, 35-46.
- Charnov, E. L. (1982). *The Theory of Sex Allocation*. Princeton University Press, Princeton.
- (1986a). An optimisation principle for sex allocation in a temporally varying environment. *Heredity*, **56**, 119-21.
- (1986b). Life history evolution in a 'recruitment population': why are adult mortality rates constant? *Oikos*, **47**, 129-34.
- and Schaffer, W. M. (1973). Life-history consequences of natural selection: Cole's result revisited. *Am. Naturalist*, **107**, 791-3.
- Chesson, P. L. (1985). Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoret. Pop. Biol.* **28**, 263-87.
- (1986). Environmental variation and the coexistence of species. In *Community Ecology* (ed. J. Diamond and T. J. Case), pp. 240-56. Harper and Row, New York.
- and Case, T. J. (1986). Overview: nonequilibrium community theories: chance, variability, history and coexistence. In *Community Ecology* (ed. J. Diamond and T. J. Case), pp. 229-39. Harper and Row, New York.
- and Warner, R. R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *Am. Naturalist*, **117**, 923-43.
- Christiansen, F. B. (1974). Sufficient conditions for protected polymorphism in a subdivided population. *Am. Naturalist*, **108**, 157-66.
- (1975). Hard and soft selection in a subdivided population. *Am. Naturalist*, **109**, 11-19.

- (1985). Selection and population regulation with habitat variation. *Am. Naturalist*, **126**, 418–29.
- Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *J. Theoret. Biol.* **12**, 119–29.
- (1967). Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. *J. Theoret. Biol.* **16**, 1–14.
- (1968). A general model of optimal reproduction in a randomly varying environment. *J. Ecol.* **56**, 219–28.
- (1970). A theoretical model for the optimal timing of diapause. *Am. Naturalist*, **104**, 389–400.
- Cole, L. C. (1954). The population consequences of life history phenomena. *Q. Rev. Biol.* **29**, 103–7.
- Comins, H. N., and Noble, I. R. (1985). Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. *Am. Naturalist*, **126**, 706–23.
- Cooper, W. S., and Kaplan, R. H. (1982). Adaptive 'coin-flipping': a decision-theoretic examination of natural selection for random individual variation. *J. Theoret. Biol.* **94**, 135–51.
- Danks, H. V. (1983). Extreme individuals in natural populations. *Bull. Entomol. Soc. Am.* **29**, 41–6.
- Dempster, E. R. (1955). Maintenance of genetic heterogeneity. *Cold Spring Harbor Symp. Quant. Biol.* **20**, 25–32.
- den Boer, P. J. (1968). Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica*, **18**, 165–94.
- (1981). On the survival of populations in a heterogeneous and variable environment. *Oecologia*, **50**, 39–53.
- Denno, R. F., and Dingle, H. (eds.) (1981). *Insect Life History Patterns: Habitat and Geographic Variation*. Springer Verlag, New York.
- Diamond, J. M. (1975). Assembly of species communities. In *Ecology and Evolution of Communities* (ed. M. L. Cody and J. M. Diamond), pp. 342–444. Harvard University Press, Cambridge, Mass.
- Dingle, H. (1981). Geographic variation and behavioral flexibility in milkweed bug life histories. In *Insect Life History Patterns: Habitat and Geographic Variation* (ed. R. S. Denno and H. Dingle), pp. 57–73. Springer Verlag, New York.
- and Baldwin, J. D. (1983). Geographic variation in life histories: a comparison of tropical and temperate milkweed bugs (*Oncopeltus*). In *Diapause and Life Cycle Strategies in Insects* (ed. V. K. Brown and I. Hodek), pp. 143–65. Junk Publishers, The Hague.
- Ellner, S. (1985a). ESS germination strategies in randomly varying environments. I. Logistic-type models. *Theoret. Pop. Biol.* **28**, 50–79.
- (1985b). ESS germination strategies in randomly varying environments. II. Reciprocal yield-law models. *Theoret. Pop. Biol.* **28**, 80–116.
- and Shmida, A. (1981). Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia*, **51**, 133–44.
- Endler, J. A. (1977). *Geographic Variation, Speciation, and Clines*. Princeton University Press, Princeton.
- Felsenstein, J. (1976). The theoretical population genetics of variable selection and migration. *Ann. Rev. Genet.* **10**, 253–80.
- (1979). r- and K-selection in a completely chaotic population model. *Am. Naturalist*, **113**, 499–510.

- Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Freas, K. E., and Kemp, P. R. (1983). Some relationships between environmental reliability and seed dormancy in desert annual plants. *J. Ecol.* **71**, 211–17.
- Gadgil, M., and Bossert, W. (1970). Life history consequences of natural selection. *Am. Naturalist*, **104**, 1–24.
- Giesel, J. T. (1976). Reproductive strategies as adaptations to life in temporally heterogeneous environments. *Ann. Rev. Ecol. Syst.* **7**, 57–79.
- Gillespie, J. H. (1973). Polymorphism in random environments. *Theoret. Pop. Biol.* **4**, 193–5.
- (1974a). Natural selection for within-generation variance in offspring number. *Genetics*, **76**, 601–6.
- (1974b). Polymorphism in patchy environments. *Am. Naturalist*, **108**, 145–51.
- (1975). The role of migration in the genetic structure of populations in temporally and spatially varying environments. I. Conditions for polymorphism. *Am. Naturalist*, **109**, 127–35.
- (1977). Natural selection for variance in offspring numbers: a new evolutionary principle. *Am. Naturalist*, **111**, 1010–14.
- (1981). The role of migration in the genetic structure of populations in temporally and spatially varying environments. III. Migration modification. *Am. Naturalist*, **117**, 223–33.
- Goodman, D. (1984). Risk spreading as an adaptive strategy in iteroparous life histories. *Theoret. Pop. Biol.* **25**, 1–20.
- Haldane, J. B. S. (1930). A mathematical theory of natural and artificial selection. VI. Isolation. *Proc. Camb. Phil. Soc.* **26**, 220–30.
- (1962). Conditions for a stable polymorphism at an autosomal locus. *Nature*, **193**, 1108.
- and Jayakar, S. D. (1963). Polymorphism due to selection of varying direction. *J. Genet.* **58**, 237–42.
- Hamilton, W. D. (1982). Pathogens as causes of genetic variation in their host populations. In *Population Biology of Infectious Diseases* (ed. R. M. Anderson and R. M. May), pp. 269–96. Dahlem Konferenzen 1982, Springer Verlag, Berlin.
- Hartl, D. L., and Cook, R. D. (1973). Balanced polymorphisms of quasineutral alleles. *Theoret. Pop. Biol.* **4**, 163–72.
- (1976). Stochastic selection and the maintenance of genetic variation. In *Population Genetics and Ecology* (ed. S. Karlin and E. Nevo), pp. 593–615. Academic Press, New York.
- Hastings, A., and Caswell, H. (1979). Role of environmental variability in the evolution of life history strategies. *Proc. Nat. Acad. Sci. USA*, **76**, 4700–3.
- Hedrick, P. W. (1983). *Genetics of Populations*. Science Books International, Boston.
- Ginevan, M. E., and Ewing, E. P. (1976). Genetic polymorphism in heterogeneous environments. *Ann. Rev. Ecol. Syst.* **7**, 1–32.
- Horn, H. S. (1975). Markovian processes of forest succession. In *Ecology and Evolution of Communities* (ed. M. L. Cody and J. M. Diamond), pp. 196–211. Harvard University Press, Cambridge, Mass.
- Hubbell, S. P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, **203**, 1299–309.
- and Foster, R. B. (1986). Biology, chance, and history and the structure of tropical rain forest tree communities. In *Community Ecology* (ed. J. Diamond and T. J. Case), pp. 314–29. Harper and Row, New York.
- Istock, C. A. (1981). Natural selection and life history variation: theory plus lessons

- from a mosquito. In *Insect Life History Patterns: Habitat and Geographic Variation* (ed. R. F. Denno and H. Dingle), pp. 113–27. Springer Verlag, New York.
- Kaplan, R. H., and Cooper, W. S. (1984). The evolution of developmental plasticity in reproductive characteristics: an application of the 'adaptive coin-flipping' principle. *Am. Naturalist*, **123**, 393–410.
- Karlin, S., and Campbell, R. B. (1981). The existence of a protected polymorphism under conditions of soft as opposed to hard selection in a multideme population system. *Am. Naturalist*, **117**, 262–75.
- and Lessard, S. (1986). *Theoretical Studies on Sex Ratio Evolution*. Princeton University Press, Princeton.
- and Liberman, U. (1974). Random temporal variation in selection intensities: case of large population size. *Theoret. Pop. Biol.* **6**, 355–82.
- Kidwell, J. F., Clegg, M. T., Stewart, F. M., and Prout, T. (1977). Regions of stable equilibria for models of differential selection in the two sexes under random mating. *Genetics*, **85**, 171–83.
- Krombein, K. V. (1967). *Trap-nesting Wasps and Bees: Life Histories, Nests and Associates*. Smithsonian Press, Washington, D.C.
- Leigh, E. G. (1975). Population fluctuations, community stability, and environmental variability. In *Ecology and Evolution of Communities* (ed. M. L. Cody and J. M. Diamond), pp. 51–73. Harvard University Press, Cambridge, Mass.
- Leon, J. A. (1985). Germination strategies. In *Evolution, Essays in Honour of John Maynard Smith* (ed. P. J. Greenwood, P. H. Harvey, and M. Slatkin), pp. 129–42. Cambridge University Press, Cambridge.
- Levene, H. (1953). Genetic equilibrium when more than one ecological niche is available. *Am. Naturalist*, **87**, 331–3.
- Levin, S. A., Cohen, D., and Hastings, A. (1984). Dispersal strategies in patchy environments. *Theoret. Pop. Biol.* **26**, 165–91.
- Levins, R. (1962). Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *Am. Naturalist*, **96**, 361–73.
- (1963). Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. *Am. Naturalist*, **97**, 75–90.
- (1968). *Evolution in Changing Environments*. Princeton University Press, Princeton.
- (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* **15**, 237–40.
- (1970). Extinction. In *Some Mathematical Problems in Biology: Lectures on Mathematics in the Life Sciences*, vol. 2 (ed. M. Gerstenhaber), pp. 77–107. American Mathematical Society, Providence, R.I.
- (1979). Coexistence in a variable environment. *Am. Naturalist*, **114**, 765–83.
- and MacArthur, R. (1966). The maintenance of genetic polymorphism in a spatially heterogeneous environment: variations on a theme by Howard Levene. *Am. Naturalist*, **100**, 585–9.
- Lewontin, R. C. (1974). *The Genetic Basis of Evolutionary Change*. Columbia University Press, New York.
- (1985). Population genetics. In *Evolution, Essays in Honour of John Maynard Smith* (ed. P. J. Greenwood, P. H. Harvey, and M. Slatkin), pp. 3–18. Cambridge University Press, Cambridge.
- Li, C. C. (1955). The stability of an equilibrium and the average fitness of a population. *Am. Naturalist*, **89**, 281–95.
- (1963). Equilibrium under differential selection in the sexes. *Evolution*, **17**, 493–6.
- Lively, C. M. (1986). Canalization versus developmental conversion in a spatially variable environment. *Am. Naturalist*, **128**, 561–72.

- MacArthur, R. H. (1965). Ecological consequences of natural selection. In *Theoretical and Mathematical Biology* (ed. T. H. Waterman and H. J. Morowitz), pp. 388–97. Blaisdell, New York.
- and Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- MacSwain, J. W. (1958). Longevity of some anthropoid bee larvae. *Pan-Pac. Entomol.* **34**, 40.
- May, R. M. (1973). Stability in randomly fluctuating versus deterministic environments. *Am. Naturalist*, **107**, 621–50.
- Maynard Smith, J. (1962). Disruptive selection, polymorphism and sympatric speciation. *Nature*, **195**, 60–2.
- (1966). Sympatric speciation. *Am. Naturalist*, **100**, 637–50.
- (1970). Genetic polymorphism in a varied environment. *Am. Naturalist*, **104**, 487–90.
- (1978). *The Evolution of Sex*. Cambridge University Press, Cambridge.
- (1982). *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- and Hoekstra, R. (1980). Polymorphism in a varied environment: how robust are the models? *Genet. Res.* **35**, 45–57.
- Mock, D. W. (1984). Infanticide, siblicide, and avian nestling mortality. In *Infanticide: Comparative and Evolutionary Perspectives* (ed. G. Hausfater and S. Blaffer Hrdy), pp. 3–30. Aldine, New York.
- Murphy, G. I. (1968). Pattern in life history and the environment. *Am. Naturalist*, **102**, 391–403.
- Orzack, S. H. (1985). Population dynamics in variable environments. V. The genetics of homeostasis revisited. *Am. Naturalist*, **125**, 550–72.
- Owen, A. R. G. (1953). A genetical system admitting of two distinct stable equilibria under natural selection. *Heredity*, **7**, 97–102.
- Palmblad, I. G. (1969). Population variation in germination of weedy species. *Ecology*, **50**, 746–8.
- Parker, F. D. (1980). Nests of *Osmia marginipennis* Cresson with a description of the female. *Pan-Pac. Entomol.* **56**, 38–42.
- (1984). The nesting biology of *Osmia (Trichinosmia) laticulcata* Michener. *J. Kans. Entomol. Soc.* **57**, 430–6.
- Powell, J. A. (1974). Occurrence of prolonged diapause in ethmiid moths. *Pan-Pac. Entomol.* **50**, 220–5.
- Prout, T. (1968). Sufficient conditions for multiple niche polymorphism. *Am. Naturalist*, **102**, 493–6.
- Real, L. A. (1980). Fitness, uncertainty, and the role of diversification in evolution and behavior. *Am. Naturalist*, **115**, 623–38.
- Ritland, K. (1983). The joint evolution of seed dormancy and flowering time in annual plants living in variable environments. *Theoret. Pop. Biol.* **24**, 213–43.
- Roff, D. A. (1974). A comment on the number of factors model of Reddingius and den Boer. *Am. Naturalist*, **108**, 391–3.
- Roughgarden, J. (1971). Density-dependent natural selection. *Ecology*, **52**, 453–68.
- Rubenstein, D. I. (1982). Risk, uncertainty, and evolutionary strategies. In *Current Problems in Sociobiology* (ed. King's College Sociobiology Group), pp. 91–111. Cambridge University Press, Cambridge.
- Sale, P. F. (1977). Maintenance of high diversity in coral reef fish communities. *Am. Naturalist*, **111**, 337–59.
- (1978). Coexistence of coral reef fishes—a lottery for living space. *Environ. Biol. Fishes*, **3**, 85–102.

- Schaffer, W. M. (1974). Optimal reproductive effort in fluctuating environments. *Am. Naturalist*, **108**, 783–90.
- and Gadgil, M. D. (1975). Selection for optimal life histories in plants. In *Ecology and Evolution of Communities* (ed. M. L. Cody and J. M. Diamond), pp. 142–57. Harvard University Press, Cambridge, Mass.
- Seger, J. (1985a). Intraspecific resource competition as a cause of sympatric speciation. In *Evolution, Essays in Honour of John Maynard Smith* (ed. P. J. Greenwood, P. H. Harvey, and M. Slatkin), pp. 43–53. Cambridge University Press, Cambridge.
- (1985b). Unifying genetic models for the evolution of female choice. *Evolution*, **39**, 1185–93.
- and Trivers, R. (1986). Asymmetry in the evolution of female mating preferences. *Nature*, **319**, 771–3.
- Shapiro, A. M. (1979). The phenology of *Pieris napi microstriata* (Lepidoptera: Pieridae) during and after the 1975–77 California drought, and its evolutionary significance. *Psyche*, **86**, 1–10.
- Silvertown, J. (1984). Phenotypic variety in seed germination behavior: the ontogeny and evolution of somatic polymorphism in seeds. *Am. Naturalist*, **124**, 1–16.
- (1985). When plants play the field. In *Evolution, Essays in Honour of John Maynard Smith* (ed. P. J. Greenwood, P. H. Harvey, and M. Slatkin), pp. 144–53. Cambridge University Press, Cambridge.
- Slatkin, M. (1974a). Competition and regional coexistence. *Ecology*, **55**, 128–34.
- (1974b). Hedging one's evolutionary bets. *Nature*, **250**, 704–5.
- Smith, F. E. (1972). Spatial heterogeneity, stability, and diversity in ecosystems. *Proc. Connecticut Acad. Sci.* **44**, 307–36.
- Stearns, S. C. (1976). Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51**, 3–47.
- (1977). The evolution of life history traits: a critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst.* **8**, 145–71.
- (1982). The role of development in the evolution of life histories. In *Evolution and Development* (ed. J. T. Bonner), pp. 237–58. Dahlem Konferenzen 1982, Springer Verlag, Berlin.
- and Crandall, R. E. (1981). Bet-hedging and persistence as adaptations of colonizers. In *Evolution Today, Proceedings of the Second International Congress of Systematic and Evolutionary Biology* (ed. G. G. E. Scudder and J. L. Reveal), pp. 371–83. Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh.
- Stephens, D. W., and Krebs, J. R. (1987). *Foraging Theory*. Princeton University Press, Princeton.
- Strong, D. R. (1986). Density vagueness: abiding the variance in the demography of real populations. In *Community Ecology* (ed. J. Diamond and T. J. Case), pp. 257–68. Harper and Row, New York.
- Sunose, T. (1978). Studies on extended diapause in *Hasegawia sasacola* Monzen (Diptera, Cecidomyiidae) and its parasites. *Kontyu*, **46**, 400–15.
- Tallamy, D. W., and Denno, R. S. (1981). Alternative life history patterns in risky environments: an example from lacebugs. In *Insect Life History Patterns: Habitat and Geographic Variation* (ed. R. S. Denno and H. Dingle), pp. 129–47. Springer Verlag, New York.
- Tauber, C. A., and Tauber, M. J. (1982). Evolution of seasonal adaptations and life history traits in *Chrysopa*: response to diverse selective pressures. In *Evolution and Genetics of Life Histories* (ed. H. Dingle and J. P. Hegmann), pp. 51–72. Springer Verlag, New York.

- Tauber, M. J., Tauber, C. A., and Masaki, S. (1986). *Seasonal Adaptations of Insects*. Oxford University Press, Oxford.
- Taylor, F. (1980). Optimal switching to diapause in relation to the onset of winter. *Theoret. Pop. Biol.* **18**, 125–33.
- (1986a). The fitness functions associated with diapause induction in arthropods. I. The effects of age structure. *Theoret. Pop. Biol.* **30**, 76–92.
- (1986b). The fitness functions associated with diapause induction in arthropods. II. The effects of fecundity and survivorship on the optimum. *Theoret. Pop. Biol.* **30**, 93–110.
- Templeton, A. R., and Levin, D. A. (1979). Evolutionary consequences of seed pools. *Am. Naturalist*, **114**, 232–49.
- Torchio, P. F., and Tepedino, V. J. (1982). Parsivoltinism in three species of *Osmia* bees. *Psyche*, **89**, 221–38.
- Venable, D. L. (1985). The evolutionary ecology of seed heteromorphism. *Am. Naturalist*, **126**, 577–95.
- Burques, A., Corral, G., Morales, E., and Espinosa, F. (1987). The ecology of seed heteromorphism in *Heterosperma pinnatum* in central Mexico. *Ecology*, **68**, 65–76.
- and Lawlor, L. (1980). Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia*, **46**, 272–82.
- Verner, J. (1965). Selection for the sex ratio. *Am. Naturalist*, **99**, 419–21.
- Via, S., and Lande, R. (1985). Genotype-environment interactions and the evolution of phenotypic plasticity. *Evolution*, **39**, 505–22.
- Walker, T. J. (1986). Stochastic polyphenism: coping with uncertainty. *Fl. Entomol.* **69**, 46–62.
- Walsh, J. B. (1984). Hard lessons for soft selection. *Am. Naturalist*, **124**, 518–26.
- Warner, R. R., and Chesson, P. L. (1985). Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Naturalist*, **125**, 769–87.
- Westoby, M. (1981). How diversified seed germination behavior is selected. *Am. Naturalist*, **118**, 882–5.
- Williams, G. C. (1966). *Adaptation and Natural Selection*. Princeton University Press, Princeton.
- (1975). *Sex and Evolution*. Princeton University Press, Princeton.
- (1979). The question of adaptive sex ratio in outcrossed vertebrates. *Proc. Roy. Soc. Lond. Ser. B*, **205**, 567–80.