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## Risk, uncertainty and evolutionary strategies

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### Introduction

Biologists have long appreciated that animals live in habitats that are spatially heterogeneous and that change over time. That most biologists subscribe to the view of natural selection favouring individuals that obtain the highest *expected* lifetime reproductive success, or genotypes which leave, *on average*, the most mature offspring, shows they also believe this variation plays an important role in evolution. Yet this belief is not echoed in most models of the evolutionary process. Apart from some models of life history evolution (Cohen, 1966, 1968; MacArthur, 1972; and Schaffer, 1974), the role of environmental variation has largely been ignored by implicitly assuming that strategies always manifest their expected fitness. In effect, the certainty of obtaining an average reward has been substituted for the uncertainty of obtaining any one of a variety of rewards.

Such a change raises the question of whether it is possible to de-emphasise the role of environmental variation in the evolutionary process without distorting our understanding of the process. An elegant analysis by Gillespie (1977) suggests that the answer is likely to be no. When he compared genotypes with the same expected reproductive success he found that natural selection favoured those with the smallest variances in reproductive success. The implication is clear: behaviour maximising average fitness may not always be the best strategy that an animal can choose. Much will depend on how environmental variation affects the likelihood of a strategy actually manifesting its expected fitness.

The purpose of this chapter is to investigate how risk and uncertainty affect behavioural decision-making and optimal patterns of resource allocation. I begin by examining the relationship between expected payoffs and their variances, and develop a fitness measure based on this relationship.

Then I use these concepts to investigate how environmentally induced uncertainty affects strategies of reproduction, foraging and social interaction.

### **From determinism to uncertainty: a general model**

The model is based on the assumption that at any point in time an animal will have a limited amount of resources ( $R_0$ ) that can be invested in a variety of activities. If the activity adopted is unaffected by the vagaries of nature this investment will result in  $\phi(R_0)$  units of fitness. Otherwise, if the strategy is sensitive to environmental fluctuations then the amount actually converted to fitness may be more or less than  $R_0$ . As a consequence the fitness of such a strategy would be  $E[\phi(R_0)]$ , the expected value of the various fitness possibilities.

For the purpose of the general model it does not really matter whether the individual's investment is used to increase fitness by increasing its own survival prospects, by increasing those of its existing offspring or other relatives, or even by producing offspring now or in the future. What does matter, however, is the form of the relationship between the appropriate fitness measure and the level of resource investment. The most realistic form of this relationship will be S-shaped (Fig. 5.1). This means that although increased investment always increases fitness ( $\phi'(R_0) > 0$ ) the rate at which fitness changes with additional investment varies. What begins as a gradual increase in fitness accelerates as investment is further increased, but eventually declines as investment levels become extremely high. Such sigmoid curves have mathematical properties such that to the left of the inflexion point each additional unit of investment brings increasing returns ( $\phi''(R_0) > 0$ ), whereas to the right of the inflexion point each additional unit brings diminishing returns ( $\phi''(R_0) < 0$ ). It appears that most animals are operating in the range of diminishing returns (Smith & Fretwell, 1974; Wilbur, 1977), but exceptions do occur and will be particularly illuminating.

Given this fitness characterisation we are now in a position to examine how environmental uncertainty affects animals confronted with only two strategies: one in which the payoff is certain and the other in which the payoff is not. In one of the simplest situations an animal has the option of investing its  $R_0$  resources in a strategy which will yield exactly  $R_1$  resources at the end of the time period, or in another strategy which will yield, with equal probability, either  $R_1 + \gamma$  or  $R_1 - \gamma$  resources at the end of the time period. On average, the 'risky' strategy will yield  $R_1$  resources, the same payoff as the 'certain' strategy. The fitnesses of the certain and risky

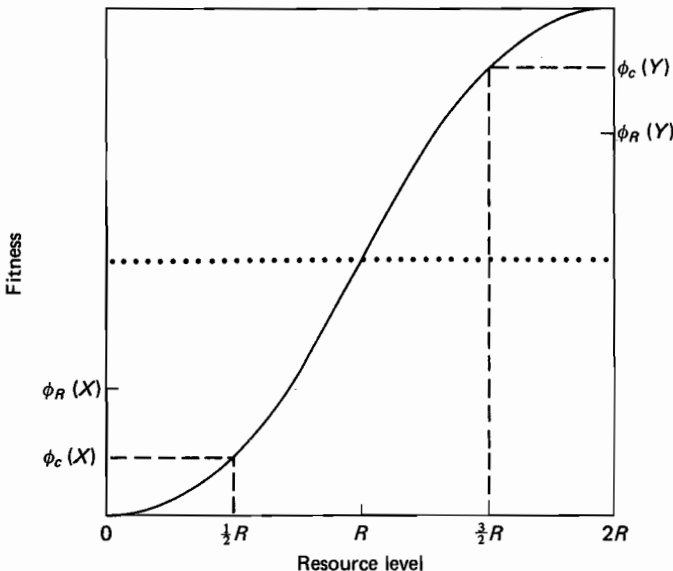
strategies are  $\phi(R_1)$  and  $\frac{1}{2}\phi(R_1 + \gamma) + \frac{1}{2}\phi(R_1 - \gamma)$  respectively. According to Jensen's inequality (Breimen, 1968) when the fitness function is concave ( $\phi''(R_1) < 0$ ), which will occur to the right of the inflexion point,  $\phi[E(R_1)] > E[\phi(R_1)]$ . Hence,

$$\phi(R_1) > \frac{1}{2}\phi(R_1 + \gamma) + \frac{1}{2}\phi(R_1 - \gamma). \tag{1}$$

Thus when animals face the prospects that increasing investments will increase fitness but at an ever-declining rate, they should select among strategies offering the same expected fitness, the one with the lowest variance. However, when the function is convex, which will occur to the left of the inflexion point, the converse should occur as the riskier strategy will have the higher expected fitness.

These relationships can be clearly demonstrated by graphical means (Fig. 5.1). For convenience a symmetric sigmoid fitness function was chosen; its inflexion point is located on the ordinate halfway between the origin and the asymptote, and thus on the abscissa halfway between the origin and  $2R$ , the point at which the asymptote is reached. For the first

Fig. 5.1. Example of how a sigmoid fitness function affects the fitness of strategies producing payoffs with certainty and uncertainty. In situations of diminishing returns the fitness of the conservative strategy [ $\phi_c(Y)$ ] is greater than that of the risky strategy [ $\phi_R(Y)$ ]. In situations of increasing returns the risky strategy [ $\phi_R(X)$ ] is superior to the conservative one [ $\phi_c(X)$ ].



case let us consider a situation to the right of the inflexion point where the expected payoff of both strategies is  $Y = 3R/2$ , but where the risky strategy offers the prospects of obtaining payoffs of  $2R$  and  $R$  with equal probabilities. From Fig. 5.1 it is clear that in this case the fitness of the certain strategy is  $\phi_c(Y)$  and is greater than  $\phi_r(Y)$ , which is the average of  $\phi(R)$  and  $\phi(2R)$ . For the second case let us consider a situation to the left of the inflexion point in which the expected payoffs of both strategies are  $X = R/2$ , but where the payoffs of the risky strategy are either 0 or  $R$  and occur with equal frequency. Here Fig. 5.1 shows that the situation is reversed as the fitness of the certain strategy is  $\phi_c(X)$  which is less than  $\phi_r(X)$ , the average of  $\phi(0)$  and  $\phi(R)$ . Thus in one case the risky strategy has a higher fitness than the certain strategy, but in the other it does not. Apparently much depends on the relationship between the initial level of investment and expected payoff, and the position of the latter with respect to the inflexion point of the fitness function.

These results suggest a variety of consequences for the ways in which animals should behave in the face of environmental uncertainty. In one sense the model predicts that animals in good bodily condition, or in favourable environments (both conditions generating returns on investments that augment fitness but at an ever-decreasing rate) should not adopt risky strategies – those offering high losses as well as high gains – if they only provide the same average payoffs as a certain strategy. In another sense the model predicts that animals should switch from risk-averting to risk-favouring strategies as their bodily condition or the favourableness of the environment declines. As long as initial resource levels or payoffs remain to the right of the inflexion point animals should attempt to reduce their decline or increase their reserves by shunning risky strategies. But as soon as initial resource levels or payoffs drop below this critical point animals should abandon conservative investment strategies and adopt those offering prospects of higher than average payoffs.

In the real world few strategies offer payoffs with certainty. In most situations animals will have to choose among strategies differing not only in their expected payoffs, but in their distribution of payoffs as well. How animals make such strategic decisions can best be seen by characterising a strategy's fitness in terms of its payoff expectation as well as its variance.

In effect, the fitness of any strategy producing a range of unpredictably occurring outcomes is simply the sum of the products of the fitness of each payoff and its weighting factor as measured by its likelihood of occurrence. Thus where the payoff of a strategy is a random variable whose expectation can be represented by  $E(X)$  the fitness of the strategy is

$$w(X) = \int_{-\infty}^{\infty} \phi(x)f(x)dx = E[\phi(X)]. \quad (2)$$

Here  $f(x)$  is a normal probability density function of  $X$  with expectation  $\mu$  and variance  $\sigma^2$ . If the sigmoid fitness function  $\phi(x)$  is represented as a normal cumulative distribution  $G(x)$ , the analysis is greatly simplified. When this is done the fitness of the strategy becomes

$$w(X) = \int_{-\infty}^{\infty} G(x)f(x)dx. \quad (3)$$

After expanding  $G(x)$  about the mean ( $x = \mu$ ) (see Appendix I for details), the fitness of the risky strategy simplifies to

$$w(X) = \phi(\mu) + \frac{1}{2}\sigma^2\phi''(\mu). \quad (4)$$

This fitness characterisation shows exactly how variance affects a strategy's fitness. If we assume that most animals operate in the range of investment levels where diminishing returns occur ( $\phi''(\mu) < 0$ ), then any change of strategy that leaves the expected payoff unchanged but increases the variance will reduce the fitness of that strategy. The most important point to note about (4) is that both mean and variance considerations are often likely to be of the same order of magnitude. Hence selection for minimising the uncertainty surrounding a strategy's expected payoff should be no less strong than that for maximising a strategy's expected payoff.

Few data have been collected that demonstrate that animals adopt behavioural strategies specifically to minimise the effects of uncertainty. But much circumstantial evidence suggests that one of the main effects of natural selection has been the evolution of adaptations, such as behavioural diversification, storage of resources, increases in body size, and increases in mobility, that buffer animals against the effects of fluctuating environments. In times of uncertainty animals often diversify their behaviour to reduce risk. Some foraging animals become generalists sampling from a wider range of food types than they otherwise would (Oster & Heinrich, 1976) and some reproducing plants set a greater proportion of seeds that will lie dormant than they otherwise would (Cohen, 1966). Presumably diversifying investment greatly reduces the variance about a strategy's expectation. Whether such diversification yields lower expected payoffs than non-diversification is presently unknown but worth investigating.

Other animals reduce risk by adopting strategies that involve resource storage. One of the most compelling examples involves marine zooplank-

ton (Bevison, Lee & Nevenzel, 1972; Lee, 1975). In seasonal environments some species invest a significant proportion of their energy acquired during periods of resource abundance in the production of wax esters. Later, during periods of resource shortage, these are utilized for energy. In less seasonal environments, zooplankton are rarely seen accumulating wax esters. Again this increased homeostasis reduces the impact of environmental variability, and it may also be achieved with a reduction in the expected payoff.

The evolution of larger body sizes may also represent a long-term response to changes in the magnitude of seasonally induced environmental uncertainty. Although an animal's absolute energy requirements increase with increases in size, the weight-specific, or relative energy requirements, show the opposite trend. Jarman (1974) and Bell (1971) argue that these relationships enable large animals to subsist on lower quality vegetation than smaller animals, as long as they can consume and process it in large quantities. One consequence of being able to utilise abundant sources of low-quality vegetation is that the pressure for animals to forage selectively is relaxed. As a result even in changing environments the probability is high that alternative low-quality food types will be available. Even if they are not available locally, increases in body size reduce the energetic constraints on travelling long distances to obtain these alternative foods (Penny-cuick, 1979). Large size then may have evolved in part because it enabled diversification of behaviour in response to fluctuating environments. Boyce (1979) has even suggested that Bergman's rule – the average increase in mammalian body size with increasing latitude – is a consequence of the increasing seasonality that also increases with increasing latitude.

The fitness function (4) also suggests that when two strategies differ both in their expected payoff and their variances, situations are likely to occur in which the strategy with the higher fitness will have the lower expected payoff. That is,

$$\phi(\mu_1) + \frac{1}{2}\sigma_1^2\phi''(\mu_1) > \phi(\mu_2) + \frac{1}{2}\sigma_2^2\phi''(\mu_2) \quad (5)$$

but where  $\phi(\mu_2) > \phi(\mu_1)$ . Obviously for this situation to arise reductions in the mean payoff must be offset by reductions in the variance. To determine how extensive the changes in expectations must be to offset changes in variance, and vice versa, we can examine the slope and curvature of the line connecting strategies exhibiting equivalent fitnesses but having different means and variances. After some manipulation (see Appendix II for de-

tails), we can show that the slope of this line is

$$\left(\frac{\partial\mu}{\partial\sigma}\right)_{w(\mu)} = \frac{-\phi''(\mu)\sigma}{\phi'(\mu)}, \quad (6)$$

and that its curvature is

$$\left(\frac{\partial^2\mu}{\partial\sigma^2}\right)_{w(\mu)} = \frac{-\phi'''(\mu)}{\phi''(\mu)} \quad (7)$$

In most biological circumstances  $\phi''(\mu) < 0$  and  $\phi'''(\mu) > 0$  (see Appendix I for the case in which  $\phi(X)$  is represented by a normal cumulative frequency distribution). Therefore  $(\partial\mu/\partial\sigma)_{w(\mu)} > 0$  and  $(\partial^2\mu/\partial\sigma^2)_{w(\mu)} > 0$ . This means that for strategies manifesting identical fitnesses, those with larger variances must also have disproportionately larger means. It also means that strategies which significantly reduce variation can tolerate even larger reductions in their expectations and still be equally successful alternatives. That equally successful alternative strategies can have different expected payoffs is an important consequence of this analysis. For the most part, behavioural ecologists evaluate the adaptive value of alternative patterns of behaviour that so often appear within populations (Maynard Smith, 1976; Rubenstein, 1980; Dunbar, 1981) solely in terms of expected payoffs. Because differences in variance can have significant effects on a strategy's adaptive value, the previous criteria are no longer sufficient. Doubtless, accounting for variance will make the field worker's task more difficult. Fortunately, equation (7) specifies quantitatively exactly how large these compensatory shifts must be in order to maintain equality among strategies. This should prevent all compensatory changes in expectations and their variances being automatically considered as offsetting.

The purpose of developing this general model was to show how uncertainty affects fitness by unravelling the relationship between a strategy's expected payoff and the variation about this expectation. Now we will use the model to investigate how variation affects decision-making in a few specific situations.

### Reproductive strategies

Reproduction often involves the allocation of limited resources among a variety of competing processes. In this section we consider how environmental variation affects the optimal (a) allocation of resources among current versus future reproduction, (b) distribution of investment among good and bad years, and (c) dispersion of young among a few or many nests.

*Dispersal in time*

We begin by considering the reproductive behaviour of an individual having  $R_0$  resources that it can mobilise and either invest in current reproduction or store and invest in reproduction the following year. We will assume that the 'stored' reserves can in fact be used in the period between reproductive episodes in ways which increase, on average, the resources the individual will have available for reproduction the following year. As long as the animal inhabits an environment that is unpredictable there will be variation in the rate of return on the stored resources. During harsh periods the reserves will actually decline, while during mild periods they will dramatically increase.

For such an animal, in which the rate of return on the risky investment can be represented by a random variable  $X$  with  $E[X] > 0$ , its fitness for the two years would be

$$w(s) = \phi(P) + E[\phi(F)]. \quad (8)$$

Here  $P$  and  $F$  are the amounts invested in present and future reproduction respectively. Note that we are assuming that the fitness of investment in current reproduction is without uncertainty. If  $s$  represents the proportion of the  $R_0$  resources allocated for storage, then  $P = (1 - s)R_0$  and  $F = sR_0X$ . The optimal level of storage,  $s^*$ , obtains when

$$w'(s) = E[\phi'(F)X] - \phi'(P) = 0. \quad (9)$$

Given that we can find this optimal level we can ask how  $s^*$  is affected by changes in (a) the expected rate of return, (b) the dispersion about this expectation, and (c) the initial amounts of resources,  $R_0$ .

Shifting the expectation of the distribution can be accomplished simply by adding a constant to  $X$ ,  $X(c) = X + c$ . Changing the dispersion, however, is more complex but can be accomplished by adjusting  $X$  as follows,  $X(c) = X + Xc - c^2$ , where  $c = E(X)$ . (In effect, this adjustment first moves the centre of the distribution to the origin, expands the dispersion and then moves the centre back to its original position.)

Upon rewriting, (9) becomes

$$w'(s) = E[\phi'[F(c)]X(c)] - \phi'(P) = 0 \quad (10)$$

where  $F(c) = sR_0X(c)$ . Since  $dP/dc = 0$  and  $dF/dc = s[dX/dc] + X(c)[dr/dc]$ , differentiating (10) with respect to  $c$  yields

$$E[\phi''(F)\{sR_0[dX/dc] + X(c)[ds/dc]R_0\}X(c) + \phi'(F)[dX/dc]] = 0. \quad (11)$$

When this is solved for  $ds/dc$  we get



$$\frac{ds}{dc} = \frac{-E[\{sR_0\phi''(F)X(c) + \phi'(F)\}dX/dc]}{R_0E\{\phi''(F)[X(c)]^2\}}. \quad (12)$$

In the case of shifts in the expectation  $dX/dc = 1$ . And when  $\phi''(\cdot) < 0$ , the biologically important range of the fitness function, it can be shown that the denominator is negative and that the numerator is positive. Hence  $ds/dc > 0$ . For changes in dispersion, however,  $dX/dc < 0$ , and therefore  $ds/dc < 0$ . Thus whereas increases in the expected rate of return for storage increase the proportion invested in delayed reproduction, increases in the dispersion about the mean increase the proportion invested in current reproduction. So far these results parallel those of Schaffer (1974).

To see how changing the amount of resources available for investment affects the investment strategy we differentiate (10) with respect to  $R_0$ . This yields

$$\frac{ds}{dR_0} = \frac{\phi''(P)(1-s) - E[\phi''(F)X^2]s}{R_0\{E[\phi''(F)X^2] + \phi''(P)\}}. \quad (13)$$

Clearly as  $R_0$  increases the proportion invested in the risky strategy of delayed reproduction can increase, decrease, or remain unchanged. When  $\phi''(\cdot) < 0$  the denominator is negative, and at least for fitness functions represented by exponential functions the numerator is positive because  $E[\phi''(F)X^2]s > \phi''(P)(1-s)$ . Hence  $ds/dR_0 < 0$ .

This conclusion is particularly striking. It suggests that individuals in good bodily condition or with large amounts of resources to invest in reproduction should avoid investing in the risky strategy and devote a greater proportion of their resources to immediate reproduction than individuals in poorer condition. This prediction might explain why young animals and those in moderate bodily condition delay reproduction, adopt alternative mating tactics that are less costly and less risky, or even become helpers, assisting other adults in their reproduction. All three strategies enable individuals to invest greater proportion of their meagre resources in activities that will increase their chances of success in the future.

### *Reproductive timing*

If the environment changes in a regular and predictable manner then selection should favour animals that track the environment. But under such conditions should animals invest heavily in reproduction during the good years, and abstain from reproduction in bad years, or should they invest the same amount in all years? In terms of the general model should animals invest  $R_0$  in all years, or should they invest  $R_0 + y$  in good years

and  $R_0 - y$  in bad years? Intuition, as well as an analysis by MacArthur (1968), suggests that selection should favour animals that adopt the boom-bust strategy of investing all their resources in the good year, and none in the bad year. The answer, however, is not so simple, and depends on the magnitude of the yearly fluctuations.

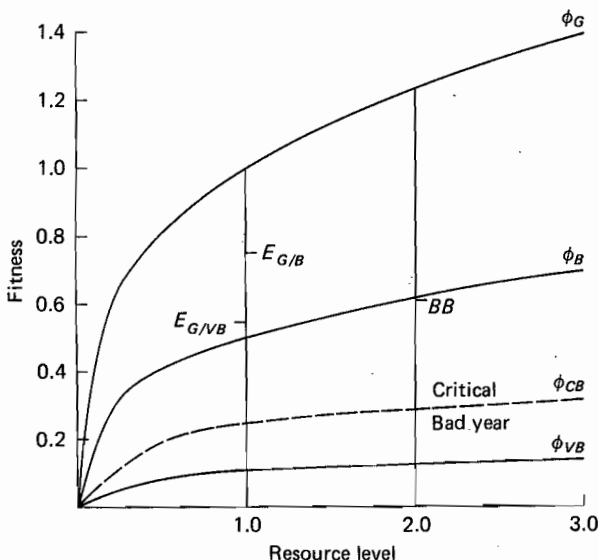
If we assume (a) that the fitness functions for good years ( $\phi_G$ ) and bad years ( $\phi_B$ ) are the same shape, only differing in their slopes and asymptotes, (b) that the level of resource investment is sufficiently high so that  $\phi''_{G \text{ or } B}(\cdot) < 0$ , and most importantly (c) that the difference between good and bad years is not too large (see Fig. 5.2), then

$$E[\phi_G(R_0) + \phi_B(R_0)] > E[\phi_G(R_0 + y) + \phi_B(R_0 - y)]. \quad (14)$$

Under such conditions animals should minimise the variance about their mean yearly investment by investing equally in good and bad years. However, if the fluctuations between good and bad years are catastrophic, then the inequality in (14) is reversed and animals should increase the variance about their mean yearly investment by adopting the boom-bust strategy. This can be shown graphically by an example in which a good year follows

Fig. 5.2. Relationships between fitness of a strategy involving constant investment in good and bad years ( $E$ ), and one involving no investment in bad years and twice the normal investment in good years ( $BB$ ).

$\phi_G(R) = R^{0.3}$ ;  $\phi_B(R) = 0.5R^{0.3}$ ;  $\phi_{VB}(R) = 0.1R^{0.3}$ ;  $\phi_{CB}(R) = 0.23R^{0.3}$ . The critical fitness function has the property that  $\phi_B(R_0) - \phi_B(R_0 - y) > \phi_G(R_0 + y) - \phi_G(R_0)$ . After rearranging, (14) results.



a bad year (Fig. 5.2). In the first case, for every unit invested, the fitness of the bad year is 50% of that of a good year. Over the two-year period the average fitness of the less variable strategy, which involves 1 unit of investment in each year, is 0.75. Over the same period, that of the more variable boom-bust strategy, which involves no investment in the bad year but 2 units in the good year, is 0.62. In the second case, the fluctuations between years is more severe and the fitness function of the very bad year is only 10% of that of a good year. Under such conditions the fitness of the boom-bust strategy is still 0.62, whereas that of the equal strategy is only 0.55.

Inspection of Fig. 5.2 shows that inequality (14) is robust and will be true for fairly severe yearly fluctuations. That the predictions of the model diverge from those of our intuition raises questions about the assumptions underlying the problem, particularly those concerning how the lack of investment in one year affects the level of investment in the following year. If, for example, an animal will be able to add on to next year's amount more than it could have invested in the bad year, then it is possible that the boom-bust strategy could be more profitable even when the difference between good and bad years is small. But because of diminishing returns much will still depend on how large this 'surplus' is. Data are therefore needed to determine exactly how environmental variation affects the accumulation of resources by 'missing out' a season.

#### *Dispersal in space*

The last question I want to consider in which variation will affect reproduction concerns strategies of nest laying – should a female lay all her eggs in one nest, or should she scatter them in a variety of nests? If her decision depends simply on each strategy's expected reproductive success, then both would yield the same fitness and she should be indifferent as to which strategy to adopt. But what if females are not attempting to maximise their average reproductive success? Suppose females are attempting to maximise the likelihood that at least one offspring survives to independence. Here the two strategies produce very different results.

If the probability of a nest escaping being preyed upon is  $s_0$  then the probability that none of a female's  $n$  nests survive is  $(1 - s_0)^n$ . This means that the probability of at least one nest surviving is  $P_s = 1 - (1 - s_0)^n$  and this increases as  $n$  increases. Clearly, animals increase their chances of being represented in the next generation by distributing their young among a variety of nests. One interesting aspect of this prediction is that this 'insurance' against extinction is acquired without diminishing average reproductive success. Another is that this principle of minimising the

likelihood of extinction is achieved by a reduction in the variance of nestling survival. As Wilbur (1977) has shown, the variance about the expected reproductive success is  $ne^2s_0(1 - s_0)$  where  $e$  is the number of eggs per nest. Thus given the fact that a female lays a fixed number of eggs, by reducing the number of eggs per nest she reduces the variance to such an extent that it offsets the increase in variance that occurs by her distributing the eggs in more nests.

To determine if a nesting strategy with the same average nestling success as another but with a smaller variance is an evolutionary stable strategy (ESS), I ran some computer simulations. According to Maynard Smith (1976), an ESS is a strategy that when rare can successfully invade a population and spread to fixation, and when fixed can resist invasion by any alternative, 'mutant' strategy. In the simulation, a female adopting the normal strategy laid 40 eggs in one nest, whereas a female adopting the mutant strategy laid 10 eggs in each of four nests. The habitat contained 100 nest sites, and the initial population consisted of one mutant and 96 normal females. Then 20 nests were chosen at random. From these all the nestlings survived to become adults. But because of nest limitations, they too were subjected to random mortality. Individuals were chosen at random and assigned one or four nests depending on their nesting strategy. When all 100 nests were occupied the cycle was completed and random nest predation began again. A total of 100 simulations were run, each beginning with a different random sequence. Both nesting strategies served as rare mutants in half the simulations, and within each series half involved moderate ( $s_0 = 0.5$ ) or high ( $s_0 = 0.2$ ) predation levels.

The results are in Table 5.1 and clearly show that the nest dispersing strategy was able to invade in about 75% of the simulations and was only displaced in about 5% of the simulations when it was common. In addition

Table 5.1. *Effects of nest predation on the fixation success of dispersed and clumped nesting strategies*

		Predation intensity			
		low		high	
		Dispersed fixates	Clumped fixates	Dispersed fixates	Clumped fixates
Clumped strategy	common	17	8	20	5
	rare	23	2	25	0

the advantage of nest dispersion seemed to increase as the intensity of predation increased. Thus it appears that reducing variance in nestling survival is an important factor that selection can operate on. The extent to which females will be able to reduce the variance in nestling mortality by increasing the number of nests they make, will depend on many other factors. The costs of making, provisioning, or frequenting more than one nest, in terms of reduced parental survival or diminished overall clutch size, and whether this behaviour increases or decreases the likelihood of each nest being taken by the predator, may be particularly relevant.

### Foraging strategies

Because foraging involves the expenditure of energy in the pursuit of even larger amounts of energy, it is a risky venture. Few animals will always succeed in acquiring more than they expend, and the likelihood of their doing so is affected by changes in the environment. The link between foraging success and fitness is indirect, but its existence means that environmentally induced variation in a strategy's rewards will affect fitness.

In fact, the general model can be applied directly to evaluate how uncertainty affects the choice of foraging strategies. Imagine animals having two foraging options: one in which the average yield over the period is fairly small, but whose distribution of gains is spread closely about the average, and another in which the average gain is slightly larger, but whose distribution of gains is spread widely about the average. In particular  $\mu_2 > \mu_1$ , and  $\sigma_2^2 > \sigma_1^2$ . According to (4), animals should choose the second more risky strategy when they are in good bodily condition ( $\phi''(\mu) < 0$ ) and  $\phi(\mu_1) - \phi(\mu_2) < \frac{1}{2}\sigma_2^2\phi''(\mu_2) - \frac{1}{2}\sigma_1^2\phi''(\mu_1)$ . But as (6) and (7) have shown, the relative advantage of the more risky strategy diminishes as the difference between the variances increases. When animals are in poor bodily condition ( $\phi''(\mu) > 0$ ) the risky strategy will always be preferable. Thus as an animal's condition changes, due either to random or consistent small events, the general model predicts that major shifts from risk-favouring to risk-averting strategies, or vice versa, are likely. It is interesting to note that in computer simulations of bird foraging behaviour Thompson, Vertinsky & Krebs (1974) showed that the formation of flocks had a stronger effect on reducing the risk of feeding failure than it did on increasing average success.

### Sociality

One of the cornerstones of sociobiology was Hamilton's (1964) development of the concept of inclusive fitness because it helped explain the evolution of altruistic behaviour. According to Hamilton, altruism would

spread as long as the ratio of the costs to the altruist divided by the benefits to the recipient were exceeded by  $r$ , the coefficient of relatedness among the two individuals. Describing relatedness has taken two forms. In one,  $r$  measures the probability that a particular gene will appear in a relative. In the other, it measures the proportion of an individual's genome represented in a relative. These two interpretations are very different, and, in fact, only the former formulation has been demonstrated to be consistent with population-genetic models of the spread of altruism in populations (Charlesworth, 1979).

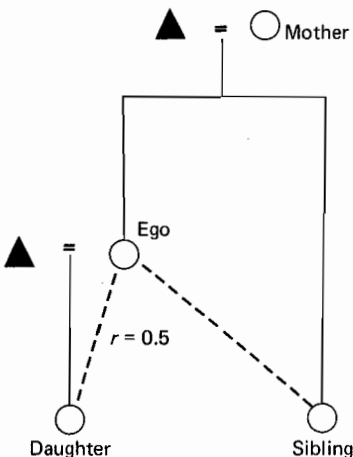
Recently Barash, Holmes & Green (1977) have shown that associated with the proportionate interpretation is the fact that relationships among relatives consisting of identical values of  $r$  may differ in the variances in the proportion of genome held in common. They cite the example that for any parent and its offspring *exactly* 50% of the genome will be shared, whereas for any two siblings only *on average* will they share 50% of their genome. This variation occurs because there is a 25% chance that two siblings will not share any genes, a 50% chance that they will share one, and a 25% chance that they will share two. Barash *et al.* suggest that one consequence of this variation is that it should significantly alter the types of altruistic behaviour shown among parents and offspring, and among siblings. They suggest that siblings should become more discriminatory, bestowing their favours on those most similar to them, and that no such discrimination should develop among parents towards their different offspring. If such discrimination could indeed happen, then there should be greater conflict among siblings than among parents and offspring.

But, as Dawkins (1979) has pointed out, even if it is unreasonable to assume that there is any linkage between genes that control recognition and the genes that predispose an individual to behave altruistically to relatives, then parents should also discriminate among those siblings possessing the altruistic gene and those that do not. An individual either does or does not possess the particular gene, and it does not matter whether the relation in question involves siblings or parents and offspring. The probability of sharing a particular piece of DNA is exactly  $\frac{1}{2}$ . Thus the variance considerations described by Barash *et al.* should not have a significant influence on the quality of social relationships among relatives.

This does not mean, however, that variance considerations do not influence the likelihood of an animal behaving altruistically to a relative, or for that matter, a non-relative. As stressed throughout this chapter investments in most activities produce uncertain returns. Assisting other individuals is no exception.

Consider a hypothetical pedigree as shown in Fig. 5.3. Given that the probability is  $\frac{1}{2}$  that Ego's prospective full sibling and prospective daughter will share with Ego a common altruistic gene, we can ask whether Ego should sacrifice its own reproduction in order to help its mother produce a sibling. Obviously, ecological factors affecting the likelihood of Ego obtaining the necessary resources to breed successfully will affect her decision. If Ego's likelihood of breeding is low then it should assist its mother who has the resources and experience to reproduce successfully (West-Eberhart 1975). As Ego's chances of success improve she should, at some point, reproduce by herself. Although this is an important consideration we will assume that Ego and her mother both have the same expectation of success. In either case, there will be uncertainty associated with the success of Ego's investment and this might lead to differences in the variance about the expected success of each strategy. If we assume that more investment increases the survival or reproductive capabilities of the newborn, but that each additional unit does so at an ever decreasing rate, then from (4) and as in Fig. 5.1, Ego should invest her resources in the strategy with the smaller variance in reproductive success. To a large extent, the strategy Ego chooses will depend on her ability to influence the effectiveness of her investment. It seems most likely that by relinquishing control over the investment to her mother a larger variance about the expected return will be produced, than by maintaining control herself. In one sense, any investment in the sibling or its mother could be manipulated by the mother and

Fig. 5.3. Hypothetical pedigree showing the relationship between Ego and its offspring and its mother's offspring.



might reduce its effectiveness from Ego's perspective. In another sense, the mother's age or experience might enable her to invest the resources more efficiently than Ego. Unless Ego can ascertain the outcome of her investment before parting with it, the variance associated with caring for her own offspring will be less than that associated with assisting her sibling. As a consequence parental care should be favoured by natural selection.

Social relationships need not occur only when relatives assist each other. Natural selection will favour cooperation and the development of sociality when all parties benefit by the interaction. It will also favour sociality that develops among strangers based on altruistic interactions as long as the altruistic act is repaid in the future either to one's self or to one's kin (Trivers, 1971). Obviously, this investment carries with it an expectation and variance about both the probability of repayment and the value of the repayment. As in (4), and the example of kin-directed altruism, when investment in strangers brings diminishing returns, individuals should assist strangers only if the altruist can reduce the variance about these two expectations. Therefore it would seem likely that such altruism would occur in closely knit groups where contact is frequent or where conflicts of interest are few, or among kin where the risk is automatically reduced to some extent simply by the increased survival or reproductive prospects of the recipient relative.

In a few circumstances, however, we might expect to see individuals increasing their fitness by behaving altruistically in situations where the uncertainties attached to the probability of repayment and the value of the repayment are high. Since the fitness function is convex for animals with few resources to invest, or those in poor bodily condition, then according to (4) their fitnesses can be increased by adopting risky strategies. It is precisely these individuals that might be favoured by adopting extreme reciprocally altruistic behaviour. If subordinate group members corresponded to this class of individuals, then we might expect them to be more altruistic than the dominants. This offers the interesting prospect that despite their very different investment strategies and their apparent conflicts of interests in many areas, on at least this issue of investment in others, their relationship is symbiotic and mutually advantageous.

### **Concluding remarks**

The aim of this chapter was to investigate whether we could ignore the role of environmental variation in the evolutionary process without distorting our understanding of the process. As the fitness characterisation (4) shows, the answer is no. For most animals in most circumstances,



increases in the variance of a strategy's outcomes will lower the fitness of that strategy. If this increased variation is accompanied by an increase in the strategy's average success, then it is possible for the strategy's fitness to remain unchanged or even increase. But, as expressions (6) and (7) show, the average increases will have to be large indeed.

In general then, animals should adopt strategies yielding small variances in their outcomes. But if animals are unable to do so by switching strategies, then they should use their resources to reduce the variance about the present strategy's expected outcome, or divert greater proportions of their resources away from the risky aspects of the strategy and invest them in those aspects with more certain outcomes, even if they have lower expected success. Exceptions to this pattern should occur, but only occasionally. Whenever animals find themselves in situations where further investments yield higher and higher returns they should choose risky strategies. Here the fitnesses of the few high-gain outcomes more than compensate for the low fitnesses associated with the rare disasters. But such conditions can only occur to the left of the inflexion point on the fitness curve, and it seems likely that selection will push this point near the origin. As a result, few animals will find themselves in this range. Nevertheless, the model indicates that some individuals, especially the disadvantaged ones, should exhibit this 'aberrant' behaviour.

At least in theory, variance considerations will have about the same impact on fitness as considerations of average success. Now it is up to field workers and experimentalists to determine whether animals behave in accordance with both considerations.

### **Summary**

1. The purpose of this chapter is to show that environmental variability can have a major impact on shaping animal investment patterns.
2. A general model is developed based on the idea that animals invest their limited resources in activities yielding payoffs that are then converted into units of fitness. In a constant environment, the payoff is certain. In a variable environment, a range of payoffs and thus fitness prospects are possible.
3. If higher payoffs produce higher fitnesses, but each payoff increment increases fitness somewhat less than the previous increment (diminishing returns), then, of strategies yielding equivalent payoff expectations, the one with the smallest variance will have the highest fitness. Conversely, if each additional payoff increment

- increases fitness somewhat more than the previous increment (increasing returns), then the situation is reversed and the strategy with the largest payoff variance will have the highest fitness.
4. Often strategies differ in both their expected payoffs and their distribution of payoffs. If two such strategies manifest equivalent fitnesses, then the one with the larger variance must have a disproportionately larger expectation. As an example, animals in good bodily condition should choose riskier foraging strategies (large payoff variances) only if the expected payoffs are very high.
  5. When animals reproduce they are faced with many investment choices. One involves animals investing some or all of their resources in current reproduction that yields a payoff with certainty, or waiting and investing their resources in future reproduction. Such a delay may increase the expected payoff, but because of the intervening period and environmental uncertainty investment in future reproduction will yield a wide range of payoffs. In such situations, increases in the dispersion of payoffs about the mean, or in the amount of resources available for investment, select for increases in the proportion of resources devoted to current as opposed to future reproduction.
  6. When environments change predictably, animals can either invest more of their resources in reproduction during the good year and less during the bad year, or they can divide the resources equally between the two. As long as the fluctuations between years are not too severe selection favours investing equally in both years. When the fluctuations are catastrophic, however, a boom-bust strategy is favoured.
  7. When nest predation is common and destroys all the eggs or nestlings present, laying all one's eggs in one nest results in the same expected reproductive success as scattering one's eggs in a variety of nests. Making multiple nests, however, lowers the variance in reproductive success and increases the likelihood that at least one offspring will survive to independence. All else being equal, making many nests is an evolutionary stable strategy.
  8. Social relationships involve investing resources in others. As a consequence, the types of social relationships that evolve will be influenced by uncertainty attached to expected payoffs. Because the variance in the effectiveness of investment in offspring is less than that in close kin, parental care will be more common than sibling care. Similarly, reciprocity should evolve most readily in

closely knit or kin groups where the variance in the probability and value of repayment is small.

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**Appendix I**

(A) Given an environment in which the outcomes of a strategy are variable, and a function  $\phi(x)$  which converts a strategy's payoff  $x$  into fitness we can represent such a strategy's fitness as the expectation

$$w(X) = \int_{-\infty}^{\infty} \phi(x)f(x)dx \tag{A1}$$

Here we assume that  $f(x)$  is a density function with mean  $\mu$ , and variance  $\sigma^2$ . Since we want  $\phi(x)$  to be sigmoid in shape, we can represent it as a cumulative distribution function  $\phi(x) = \int_{-\infty}^x g(u)du$  with mean  $m = \int_{-\infty}^{\infty} xg(x)dx$  and variance  $\sigma^2 = \int_{-\infty}^{\infty} (x - m)^2g(x)dx$ . By expanding  $\phi(x)$  about  $x = \mu$ , we get

$$w(X) = \int_{-\infty}^{\infty} \left[ \phi(\mu) + (x - \mu)\phi'(\mu) + \frac{1}{2}(x - \mu)^2\phi''(\mu) + \frac{1}{6}(x - \mu)^3\phi'''(\mu) + \frac{1}{24}(x - \mu)^4\phi^{iv}(x_1) \right] f(x)dx \tag{A2}$$

where  $x_1$  lies between  $x$  and  $\mu$ . If  $\phi(x)$  is symmetric then the odd terms in (A2) drop out, leaving

$$w(X) = \phi(\mu) + \frac{1}{2}\phi''(\mu)\sigma^2 + R \tag{A7}$$

where  $R \leq \frac{1}{24}\mu_4 \cdot \max|\phi^{iv}(X)|$ .

To find out the magnitude of  $R$  we can suppose that  $\phi(x)$  is a normal distribution function. Then  $\phi(x) = \Phi((x - m)/s) = \Phi(z)$ . Since  $\phi^{(r)}\mu = r\Phi^{(r)}((\mu - m)/s)/s$

and 
$$\Phi^{(r)}(z) = \frac{d^{r-1}}{dz^{r-1}} \cdot \frac{\exp[-z^2/2]}{(2\pi)^{\frac{1}{2}}}$$

then  $\Phi^{(iv)}(z) = (3z - z^3) \cdot \exp[-z^2/2]/(2\pi)^{\frac{1}{2}}$ . As a result  $\Phi^{(iv)}(z)$  takes on its maximum value 0.5506 at  $z = 0.72$ . The maximum error is therefore  $\frac{1}{24}\mu_4(0.5506/54) = 0.023\mu_4/s^4$ . If we assume that  $f(x)$  is normal with

mean  $\mu$ , and standard deviation  $\sigma$ , then  $\mu_4 = 3\sigma^4$  and the maximum error is  $0.0688 \left(\frac{\sigma}{s}\right)^4$ . If  $\sigma/s = \frac{1}{3}$  then  $R < 0.0076$ , which is small.

(B) Now we substitute normal density functions for  $\phi'(x)$  and  $f(x)$  to get an explicit expression for  $w(X)$ . The first three derivatives of  $\phi(x)$  are:

$$\phi'(\mu) = \frac{\exp[-(\mu - m)^2/2s^2]}{s(2\pi)^{\frac{1}{2}}};$$

$$\phi''(\mu) = \frac{-(\mu - m)\exp[-(\mu - m)^2/2s^2]}{s^3(2\pi)^{\frac{1}{2}}}$$

and 
$$\phi'''(\mu) = \left[ \frac{-1}{s^3(2\pi)^{\frac{1}{2}}} + \frac{(\mu - m)^2}{s^5(2\pi)^{\frac{1}{2}}} \right] \exp[-(\mu - m)^2/2s^2]$$

Thus where  $\mu > m$ ,  $\phi'(\mu) > 0$ ,  $\phi''(\mu) < 0$ , and  $\phi'''(\mu) > 0$ . This means that when the centre of  $f(x)$ , the payoff distribution, is to the right of the inflexion point of the fitness function ( $s$ ), increases in the dispersion of  $f(x)$  will lower  $w(X)$ .

The mathematics of this Appendix are the work of Professor H.E. Daniels and are greatly appreciated.

## Appendix II

If  $w(X) = \phi(\mu) + \frac{1}{2}\sigma^2\phi'''(\mu)$  then

$$\partial w/\partial \mu = \phi'(\mu) + \frac{1}{2}\sigma^2\phi''''(\mu), \quad \partial^2 w/\partial \mu^2 = \phi''(\mu) + \frac{1}{2}\sigma^2\phi^{iv}(\mu),$$

$$\partial w/\partial \sigma = \sigma\phi''(\mu) \text{ and } \partial^2 w/\partial \sigma^2 = \phi'''(\mu).$$

By assuming that terms of order higher than 2 will not add to fitness we can simplify and combine these partial derivatives to yield the slope

$$\frac{\partial \mu}{\partial \sigma} \approx \frac{-\phi''(\mu)\sigma}{\phi'(\mu)}$$

and curvature

$$\frac{\partial^2 \mu}{\partial \sigma^2} = \frac{-\phi'''(\mu)}{\phi''(\mu)}$$

for the line containing all strategies manifesting the same fitness,  $w(X)$ .

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