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The evolution of reproductive strategies: a commentary

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To understand the evolution of any trait, one must know both the selective forces that are operating, and the nature of the genetic variance. Usually we are ignorant of both. One attraction of studying life histories is that the traits under study contribute directly to fitness: if we know the mortality and fecundity schedules of some genotype, we know its fitness. Of course, things are not quite as easy as that, because we need to know mortality and fecundity in the wild, and not in the laboratory, but we are in better shape than we would be if, for example, we were studying courtship or fighting behaviour. Because the contributions of fecundity and longevity to fitness are so direct, the importance of trade-offs is at once obvious. If there were no trade-offs, all organisms would be as fecund as the most fecund, as long-lived as the most long-lived, and would develop as rapidly as the most rapid developer. The problem of trade-offs was mentioned in almost every paper at the symposium, and was a major topic of several – for example, the papers by Charlesworth & Morgan, and by Partridge & Sibly.

There are two ways of approaching the problem of trade-offs. To a geneticist, a trade-off manifests itself as a negative genetic correlation between two traits – for example, long-lived genotypes are less fecund – and such correlations can, at least in principle, be measured. To a physiologist, trade-offs arise from physiological interactions, and can, again in principle, be discovered by experimental manipulation. A geneticist needs to measure the matrix of genetic variances and covariances: given that, and a knowledge of the selective forces, he can predict the course of evolution. The aim of a physiologist is somewhat harder to define. In effect, one wants to know the 'phenotype set', or 'fitness set' in Levins' (1968) terminology: that is, the set of phenotypes that are possible. Given the phenotype set, and a knowledge of the selective forces, one can deduce the optimum phenotype to which the population will evolve. The snag, of course, lies in the word 'possible'. Does this mean 'possible given the genes segregating in the population at the present time', or 'possible given, not only the genes now segregating, but mutations that may arise in the future'? If it means the latter, how long a future? Were the whale and the bat in the phenotype set of the first species of eutherian mammal? In practice, one tends to think, rather imprecisely, of the range of phenotypes that could be produced by selection acting on a species in a few thousands of generations.

At first sight, the case for the genetic approach is a strong one: given the necessary genetic information, we could indeed predict the course of evolution, for a few generations, and assuming a population large enough to make drift unimportant. But the practical difficulties, even for the most favourable organisms, are formidible. We need to measure phenotypes in the wild. We must measure genetic correlations: if some individuals have a more favourable environment than others, we may find spurious positive correlations between fitness traits. We need to measure the additive component of the genetic variance: if members of a population vary in degree of homozygosity, this could give a misleading genetic correlation between sibs. Perhaps most serious of all, there is no reason to expect genetic correlations to be constant within a species; for example, correlations can arise from linkage disequilibrium caused by recent selection, and be very transitory. Indeed, one can argue that the only correlations likely to be sufficiently stable to be interesting arise from physiological interactions that could more easily be discovered by direct experimental manipulation.

There is one case in which genetic and physiological methods have been applied to the same problem, happily with consistent results. Rose & Charlesworth (1980) showed, in *Drosophila melanogaster*, a negative genetic correlation between adult female longevity, and fecundity when young. This fits with the results of physiological manipulation (Lamb 1964; Maynard Smith 1958), admittedly on a different species, *D. subobscura*, showing that a range of treatments that reduce the rate of egg-laying (including raising ovariless females from mothers homozygous for the gene *grandchildless*, and giving young adults 5000 rads of X-rays) prolong adult life. The moral, I think, is that genetic and physiological approaches can be complementary. An attempt to measure the genetic covariance matrix in the wild does not seem to me to be a sensible enterprise, but the use of genetic analysis to reveal pleiotropisms, which must have a physiological basis, can be valuable.

I first met the idea of trade-offs when working in aircraft design. If, for example, you want an aeroplane to fly fast, you give it small wings, and pay for the high speed with a long take-off run. This is all predictable, because there is a theory that relates lift and drag, and hence take-off speed and top speed, to wing area. One reason for our difficulties in life-history theory is that we do not have a comparable quantitative theory

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either of senescence or of development rate. The absence of a theory of development rate can be illustrated by our inability to answer the following questions. What places an upper limit on the rate of growth? Why is it that bacteria, in optimal conditions, can double in 20 minutes, whereas a mammalian cell, at best, takes 8 hours? It is possible to suggest answers to these questions (Maynard Smith 1969), but they are no more than plausible guesses. We are in similar difficulties over senescence. For example, suppose an animal has been selected to have a long adult life before senescence sets in; is it necessary (for example, because of the need for accurate molecular replication) that it should have a long development time? Again, we can speculate, but we do not know. The fact that, across taxa, there is a positive correlation between longevity and development time does not by itself tell us why the correlation exists.

This brings me to my final topic, the comparative method, discussed at this symposium by Harvey and Keymer. In recent years the method has been transformed: it is no longer possible to dream up a theory, and then to search the literature for a few species that fit the predictions. Through the introduction of phylogenetic reasoning and statistical analysis, we now have powerful tools for testing theories about evolution. I am not sure, however, that we are yet very good at using them. Suppose that we are satisfied that traits A and B are correlated across taxa, in the sense that, when one arises in an evolutionary lineage, the other is likely to do so. We are still a long way from a causal explanation. The two traits may be physiologically independent adaptations to the same ecological feature (herbivorous mammals are often both hypsodont and have a long alimentary canal); the two traits may be independent adaptations to two features of the environment that commonly co-occur (cold places are often covered by snow, so that mammals with thick fur are often white); trait A may be an ecological adaptation, and B a secondary adaptation entailed by A (large land mammals have relatively stout legs); two traits may be demographically linked (animals with a high juvenile mortality must have high fecundity); there may be chemical or physical constraints that cause A and B to occur together (because of the law of levers, animals that dig tend to run slowly). Doubtless there are other possibilities. The snag is that, when thinking about life histories, we lack the kind of theory (except, of course, for demography) that would enable us to make predictions like 'large land animals will have relatively stout legs'. One of the most encouraging features of the symposium, shown, for example, in the relation between the papers by Charnov and by Harvey & Keymer, was the indication that people are seeking a tie-up between models on the one hand and comparative data on the other.

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