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POLYMORPHISM AND NATURAL SELECTION

by

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A few years ago there was a small outbreak of controversial literature, appearing chiefly in the *American Naturalist*, occasioned by the criticism by two Oxford zoologists, A. J. Cain and P. M. Sheppard, of some perhaps over-confident claims made by T. Dobzhansky in the third edition of his book *Genetics and the Origin of Species*.

The three points made by Cain and Sheppard are *first*, that no sufficient definition or explanation has been given of what is meant by one population being more highly adapted than another to a particular environment. The quantity $\overline{W}$, called the "average adaptive value" by Wright, is based on comparisons among genotypes in a particular population, and cannot supply a comparison between different populations. *Secondly*, Cain and Sheppard, while admitting that if polymorphism within a breeding community increases "the efficiency of the exploitation of the resources of the environment then polymorphic organisms could be regarded as better adapted than monomorphic ones", ask for evidence of such increased exploitation, and point out that this is a conclusion which Dobzhansky has assumed. He says: "A single genotype, no matter how versatile, could hardly function with maximal efficiency in all environments. Hence, natural selection has preserved a variety of genotypes, more or less specialized, to render the organism efficient in a certain range of the existing environments." This is evidently a *non sequitur* for the second sentence gains no support from the first, and it does seem to involve a grave misunderstanding of the nature of Natural Selection to suppose, without detailed examination, that polymorphism could arise in this way.

In the *third* place Cain and Sheppard, while allowing that in the genus *Drosophila* widely ranging species do show greater polymorphism than those of narrow range, suggest that it might equally be that the wide range has been a factor favouring polymorphism as that polymorphism should be responsible for the wider range.

In a long and elaborately mathematical study Li (*Amer. Nat.* 89, pp. 281–295, 1955) is led to accept these three criticisms, and the controversy, so far as it had gone, might be considered at an end, had not he thought it necessary to accompany these admissions by somewhat vague, but aggressive, comments on the papers in

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which Cain and Sheppard had expressed their point of view; generally to the effect that they do not understand the subject on which they were writing. Seeing that the validity of their points is admitted, it seems unnecessarily ungracious for the mathematician to take this superior tone. As a defence, if defence were thought to be necessary, it is moreover ineffectual. Cain and Sheppard, for example, deplore the use, as if they were synonyms, of the words adaptive, and selective, and point to a series of authors including myself, who had taken pains to distinguish the two ideas, but Li writes:

> If the expression "adaptive value" is as misleading as claimed by Cain and Sheppard, the writer wishes to point out that Fisher (1930) in describing the same phenomenon, has employed the same phraseology (quoting)—"that is, if the heterozygote is either better or worse adapted than both the homozygotes". The only thing that has escaped the attention of Fisher is the relationship between q and $d\bar{W}/dq$.

There is in my words as quoted no trace of the confusion indicated by Cain and Sheppard. I speak of the heterozygote as better adapted than both homozygotes, not of the system of three genotypes in equilibrium as better adapted than some other possible population. Of course, if I had fallen into the same fault as Li here seems to wish to defend, it would not excuse any independent writer who is not relying on my authority, but apparently on that of Sewall Wright, as is indicated by the Parthian shot at the end of his quotation, in which quite a new subject is raised. I have never indeed written about $\bar{W}$ and its relationships, and now that the alleged relationship has been brought to my attention, I must point out that the existence of such a "potential function" as that which Wright designates by $\bar{W}$, is not a general property of natural populations, but arises only from the special and restricted cases which Wright has chosen to consider. Selective tendencies are not, in general, analogous to what mechanicians describe as a *conservative* system of forces. To assume this property is one of the gravest faults of Wright's formulation.

I should not have alluded to this storm in a tea-cup, but for the circumstance that I mean to put forward some ideas on this same problem of the possible adaptive value of polymorphisms, and incidentally, to express my personal opinion that Dobzhansky was right in regarding polymorphism as very often properly described as an adaptation to the conditions of life in which a species finds itself, but for reasons quite distinct from the direct action of Natural Selection, or at least from Natural Selection as it acts among the individuals of any one interbreeding population.

May I turn to begin with to a little-known book of nearly one hundred years ago called the *Origin of Species*. On p. 136, after pointing to the wide diversity of the varieties which human selection has produced from the same material in domestic species such as horses or pigeons, Darwin goes on:

> But how, it may be asked, can any analogous principle apply in nature. I believe it can and does apply most efficiently (though it was a long time before I saw how), from the simple circumstance that the more diversified the descendants from any one

species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers.

Darwin proceeds to illustrate his idea characteristically by drawing on facts from various fields.

From agricultural experimentation:

It has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can be raised in the latter than in the former case.

From ecological observation:

For instance I found that a piece of turf, three feet by four in size, which had been exposed for many years to exactly the same conditions, supported twenty species of plants, and these belonged to eighteen genera and to eight orders, which shows how much these plants differed from each other.

From agricultural practice:

Farmers find that they can raise most food by a rotation of plants belonging to the most different orders: nature follows what may be called a simultaneous rotation.

In these excerpts Darwin is arguing as an observational naturalist developing a general principle by the recognition of relevant analogies; it is quite the antithesis of the deductive procedure of analytic work. It serves to prepare the mind for the acceptance of his belief that Natural Selection is a process constantly favouring diversity, in a wide variety of natural circumstances; and that this tendency flows from the diversity of the innate properties of the organism required in the different particular situations in which it may find itself. The attempt to justify this conclusion deductively as a consequence of natural selection is made in the following section of eleven pages, and though I find this thoroughly convincing, it is obvious that, lacking as he did any distinct theory of inheritance, it was impossible for Darwin strictly to prove his point. He is leading towards the problem of the diversification of species within a genus, which has more recently been called "speciation", and he does not attempt any detailed discussion of how the fission of a single interbreeding population into two can be brought about.

Without the deductive basis supplied by genetical theory, however, it was quite within the competence of the general facts about heredity known to Darwin to imply that diversity in the requirements and opportunities of different environments accessible to the same species would in natural conditions exert a selective action favouring diversity, and that this would in fact tend to increase the genetic diversity of the species, with increase of population, and fuller exploitation of the natural resources of the territory. Such a change is properly called adaptive without regard to, or consideration of, the selective system which may have brought it about.

Anterior to any question of Balanced Polymorphism, therefore, there are general grounds for regarding any cause of diversity, such as polymorphism is, as carrying usually certain general advantages, which may in many cases outweigh the real drawbacks such as lowered viability, which are also undoutbtedly associated with the balanced polymorphic condition. The advantage which is most conspicuous in Darwin's discussion is that for a given population density competition between individuals of the same species will be the less severe, the more diversified are their constitutions, habits and behaviour. Whether such diversity is more advantageous in the form of a discontinuous polymorphism, rather than in the form of wider continuous variation, Darwin does not discuss.

Adaptation to the organic environment is not, however, wholly concerned about relations with organisms of the same species. Other species may be also important, as food or prey, as predators, as parasites, and so on. The relations between species, or among the whole assemblage of an ecology, may be immensely complex; and at Dr. Cavalli's invitation I propose to suggest that one way of making this intricate system intelligible to the human mind is by the analogy of games of skill, or to speak somewhat more pretentiously, of the Theory of Games.

A little more than 20 years ago (1934) I was led to rediscuss an old puzzle in the tactics of card play, which had been discussed in correspondence between Montmort and Nicolas Bernoulli early in the eighteenth century, and of which a rather full account had been given by Todhunter in his *History of the Theory of Probability.* Each of the players could have at one stage of the game known as Le Her a significant choice, but whereas it was to the advantage of A that these decisions should be alike, B had something to gain by them being unlike. No course of action seemed unequivocally advisable to a player who wished to assume that his opponent was playing as skilfully as possible, but that his own aim lay in making this skilful play as unsuccessful as might be, within his own range of choice. This general method of looking at such problems has since been called the Minimax Principle. Using it for the game of Le Her, and recognizing that it was not impossible for a player to randomize his decisions, I was able to show that for both players only a randomized strategy would satisfy the condition for playing as well as possible. One could calculate the frequencies of choice appropriate to each, and the general advantage of one of them. Ten years later (1944) the Princeton mathematicians, v. Neumann and Morgenstern, published a mathematical treatise on the Theory of Games, and developed with great generality both the Minimax Principle and the randomized, or, as they called it, the mixed strategy, to which indeed v. Neumann had earlier drawn attention in one of the German mathematical journals.

The success of a randomized strategy in games flows from the fact that the players *learn* to anticipate their opponent's customary reactions, and that the adoption of randomization introduces a new degree of uncertainty in such anticipations. A similar measure of uncertainty must be introduced into the reactions of "natural enemies" in the state of nature, especially by discontinuous variations of the kind made possible by balanced polymorphisms affecting the appearance, or the behaviour.

Now I am comparing whole species, the relations between which are antagonistic, to the players in a game of skill. Among the higher animals there can be no doubt of the important extent to which they learn by experience and adjust their tactics to the normal reactions of their adversary; and in this they are evidently analogous to human contestants at cards or chess. I believe, however, that if we considered only the factor of individual learning we should overlook the most important aspect of the application of these principles of the theory of games to ecological situations. In these each species is, through immense periods of time, evolving weapons, sense organs and innate drives in such a way among other things as progressively to improve its chances of success in these encounters. Move must alternate with countermove over millions of years. And it would appear that the evolutionary paths open to the antagonist of a polymorphic species are often none of them so profitable as those open to the enemy of a better standardized opponent. Of course, it should be admitted that the fact of exhibiting a balanced polymorphism may retard the evolutionary remodelling of its individual morphs. This in some cases it certainly may do; yet it is clear, especially in some of the polymorphic butterflies which display mimicry, that particular mimics within the assemblage must have been moulded to their existing form with the utmost nicety.

I hope I have not seemed to be dogmatic, or to be asserting sweeping generalizations. Every case must differ in some particulars from every other. I do not regard polymorphism as a *necessity*, or as a *panacea*; but I have tried to show that in favourable cases the balanced polymorphic condition, however it may have arisen, may play a serviceable part in the evolutionary life of individual species.

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