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978-0-521-54936-3 - Genes in Ecology: The 33rd Symposium of the British Ecological Society University of East Anglia

Edited by R. J. Berry, T. J. Crawford and G. M. Hewitt

Excerpt

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PART 1
GENES IN ECOLOGY

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1. GENES AND ECOLOGY IN HISTORY

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VIEWS IN OXFORD IN THE 1930s AND 1940s (A.J.C.)

Some time soon after 1945 I was rash enough to use the word *ecology* when speaking to E.B. Ford, who was not in a good mood. He glared, and remarked in his thinnest manner:

It seems to be . . .

what animals do . . .

when they are doing *nothing interesting*.

The explanation of this apparent hostility goes back to the 1930s. There is some indication that it was partly reciprocated. Charles Elton (1938) wrote, in an article entitled 'Animal numbers and adaptation':

At a time when ecology and genetics are each racing swiftly towards one new concept after another, yet with little contact of thought between the two subjects, there may be some advantage in surveying, if only synoptically and in a preliminary fashion, the largely uncharted territory between them.

He points out that Darwin had had a clear insight into the struggle for existence, but no reliable theory of variation. Geneticists, in contrast, are good on variation:

But their training and experience prevent them from knowing much about the struggle for existence in nature, that is to say, the section of ecology which deals with animal populations, competition, and similar subjects.

This, while perhaps true in general, was hard upon Ford, who had already linked type of variation and absolute numbers in his joint paper with his father on the Marsh Fritillary, *Melitaea aurinia*, in 1930, and who had collaborated, in the perhaps slightly unexpected role of protozoologist, with Elton and J.R. Baker from 1925 to 1928 in a study of the fluctuations in numbers of voles in Bagley Wood near Oxford (Elton *et al.* 1931). Elton, eminently fair-minded, goes on:

Ecologists, correspondingly, although they are being drawn into a deep study of numbers, have inclined to believe that evolution was

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long and ecology was short, that variation and the formation of new races and species take place too seldom to be of much significance in ordinary ecological studies. Generally speaking, one of the assumptions made in most ecological work is that the species will remain constant. The best field studies of the species problem have usually been done by systematists, but their results have naturally lacked the experimental analysis of variation, or the background of population research which is needed in order to discover how these interesting systematic distributions may have arisen.

Plenty of workers could echo these words today. Ecology is a more than full-time study, and enough for anyone without complicating it. So is genetics; and the complexities of applying genetics to ecology could discourage the hardiest. I suspect that it is really evolutionists, however disguised, that want to bring the two together.

In fact it was Elton, surely an ecologist if ever there was one, who, as far back as 1924 had linked fluctuations in animal numbers, or rather the smallness of populations in the troughs of cycles, with the spread of non-adaptive characters. But why did he do so? As an ecological systematist, ranging widely over many groups and species and knowing them in the field, he was deeply impressed with the impossibility of seeing any adaptive significance in so many of the characters in which related species differ. This was a very usual attitude in the 1920s, partly because of the strong emotional reaction against natural selection and 'Nature red in tooth and claw' which turned many minds to vitalism and Lamarckism and was memorably expressed by George Bernard Shaw in the preface to *Back to Methuselah*.

In his book *Animal Ecology* (1927), Elton spelt out in detail his views on non-adaptive characters, and the light that could be thrown on evolution by studies of changes in animal numbers (ch. 12, pp. 179–187):

Every biologist accepts the fact that evolution has taken place. The problem which has not yet been really solved is the exact manner in which it has happened. The existence of vast numbers of undoubted and complicated adaptations in physiological, psychological, and structural characters makes it reasonably certain that Darwin's theory of natural selection must be essentially true, however we may disagree about parts of it.

But after describing the apparent camouflage of arctic animals in their summer brown and grey coats or plumages and their winter white, he points out some 'awkward facts' which hardly fit the hypothesis of adaptive camouflage:

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All over the arctic regions the arctic fox possesses two colour phases, one of which is brown in summer and white in winter, while the other is grey or black in summer and 'blue' — often quite black — in winter. The writer has seen a 'blue' fox in summer which was the colour of a black cat, and startlingly visible against rocks and vegetation at a distance of a quarter of a mile. The blue and white phases occur equally in males and females, and interbreed freely, and in different parts of the arctic regions are found in various proportions in the population. . . . If the whiteness in winter is an adaptation, the blackness of the other phase cannot also be advantageous. If the black colour is not adaptive, *how did it evolve?* If the white colour is not adaptive, *how does the black survive?* We have in addition to reckon with the fact that in many parts of the arctic, the fox can have no possible use for its colour in winter, because it subsists at that season upon carrion left by bears, out on the frozen sea-ice, or if it is on land, it depends almost entirely on caches of animals collected and stored up in the autumn. [His italics.]

Characters, in pure Darwinian theory, can be spread only by natural selection, but if so, 'all the characters possessed by animals — at any rate those which separate closely allied species — must be of some direct use to the species' or to one sex, or be 'intimately bound up in development with some other character which is useful. . .'. This cannot be the case with the arctic (as against the red) fox, and naturalists with field experience, Elton points out, have indeed nearly all rejected the idea of colour adaptation in mammals (though not in all other groups):

It can always be argued. . . that even if the colours are not directly adaptive they may be correlated in development with some character (perhaps physiological) which *is* adaptive. But such arguments cannot apply to species which are dimorphic, like the arctic fox or the white-eared cob.

He goes on to give three other mammalian examples, to refer to Stresemann for numerous examples in birds, and to instance 'exactly comparable colour dimorphism' in some American dragonflies. That very phenomenon, therefore, which was to be used with such effect by Fisher and Ford in studies on natural selection is here shown by cogent argument and the facts of field natural history to be inexplicable by selection. But Elton knew that a far greater range of other characters have the same implications, namely all, or nearly all, the differences (non-polymorphic) between closely related species:

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There is another important line of evidence on the subject of adaptation which has recently been investigated very carefully by Richards and Robson and reviewed in a paper²⁹. The gist of their conclusions is that very closely allied species practically never differ in characters which can by any stretch of the imagination be called adaptive. If natural selection exercises any important influence upon the divergence of species, we should expect to find that the characters separating species would in many cases be of obvious survival value. But the odd thing is that although the characters which distinguish genera or distantly allied species from one another are often obviously adaptive, those separating closely allied species are nearly always quite trivial and apparently meaningless.

The reference 29 is to Richards and Robson's paper, 'The species problem and evolution', in *Nature* (1926). The argument in it was repeated in Robson's *The Species Problem* (1928), and developed with a wealth of detailed observations in Robson and Richards's *The Variation of Animals in Nature* (1936). (The species problem was not then what it is now.) Charles Elton gave especial thanks to O.W. Richards in his 1927 book for extensive help both with insect examples and in the discussion of ideas. Robson and Richards's book was highly influential, being quoted (for example) by Sewall Wright (see Provine 1986, for discussion). It deserves rather more respectful attention than it has received recently. They were as critical of Elton's and their own ideas as of other authors' — not too common a trait; they had an excellent classification of isolating mechanisms antedating Dobzhansky's; and they were rightly critical of most of the little work done on *Cepaea* to that time. Their detailed list of characters in psammocharid (pompilid) wasps showing non-adaptive differences is so similar in format and intent to that of Dobzhansky's for *Drosophila* species in his 1956 paper, 'What is an adaptive trait?', that one suspects an undocumented connection.

Nevertheless, it must be allowed that Robson and Richards showed a surprising reluctance to allow any example of natural selection; their cautious qualification that characters were non-adaptive as far as they could see became too often a certainty that they were non-adaptive; and their arguments were sometimes one-sided. Thus they allowed that some pompilid wasps were stoutly built anteriorly for digging out spiders but did *not* draw the inference that the more lightly built were adapted for ranging widely. It is as if one should say that Geoff Capes is adapted for putting the shot, but Steve Cram and Carl Lewis are not adapted for running. Their requirement that selection should be shown not merely

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to act but to have changed a character was over-rigorous when discussing the scope of selection; and at the very end of the book, they let the cat out of the bag:

In arguing that an element of self-regulation and self-organisation has had an influence [as against both natural selection and chance] in evolution we are aware that we are touching certain profound and speculative issues. If this organising activity is indeed an agent in producing the main adaptive tendencies in evolution, it might be argued that the gradual upbuilding and perfection of adaptations, because they involve so large an element of design, must also involve some reference to a purpose independent of survival value and chance, and existing as an end in itself. . . . For those who believe that all organisation is produced by the material processes envisaged by the traditional theories, the scheme of evolution must seem to be clear, at least in outline. For those with whom the difficulties we have outlined in this work have any weight, it must remain to attempt a clearer definition of the purposeful activity with which we seem confronted.

In this vitalistic or perhaps theistic attitude, Robson and Richards were far from alone. Alister Hardy, an undergraduate with Elton and J.R. Baker and later the Linacre Professor of Zoology at Oxford, was an earnest Unitarian and certainly a vitalist. Others, perhaps less extreme, limited the action of selection severely. There was in Oxford a fine tradition of work on crypsis and polymorphic mimicry in the Hope Department of Entomology, beginning with E.B. Poulton, a friend of Alfred Russel Wallace, and continued by his successor, G.D. Hale Carpenter. Yet Hale Carpenter, an ardent believer in natural selection producing crypsis and polymorphic mimicry in insects, with extensive field experience and experiment in Africa to his credit, took considerable pains to find in the collection a lepidopteran with a non-selectable character (a violet-purple sheen only to be seen by viewing the wing very obliquely) to show me, and challenged me to explain it by natural selection.

Even my supervisor John Baker, an amazing polymath and firm believer in evolution, returned our first paper on *Cepaea* to me with the remark that there were fashions in science, and sometimes it was fashionable to believe in natural selection, and sometimes it was not. When I expostulated that we had the prey, its genetically mediated variation, the predator, and a significant difference in the polymorphism in woodlands and in green habitats, he indicated that he distrusted statistics. He said he would look at the paper again (and I'm sure he did — he was a most truthful man) but it reappeared on my desk without comment.

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In Cambridge matters were even worse. The excellent naturalist W.H. Thorpe came to Oxford one year to give the Balliol lectures. A party from the Department of Zoology went to hear the first one and did not attend the rest. The lectures were on evolution, and he produced the example of the cuckoo which needs five simultaneous adaptations to function as a parasite, none of which would work unless fully developed — with the obvious conclusion that the cuckoo's adaptations could not be evolved by natural selection. He appeared totally ignorant of the Great Spotted Cuckoo which, parasitizing host-species of its own size, does not have all these adaptations. This seems to have been a popular argument in Cambridge: Charles Raven, naturalist and Regius Professor of Divinity to 1950, used it in detail in his Gifford lectures 1951–52 (pp. 137–139 in the Second Series) with the comment:

It will be seen that each one of this sequence of conditions is essential to the success of the whole. Yet each by itself is useless. The whole *opus perfectum* must have been achieved simultaneously. The odds against the random occurrence of such a series of coincidence are, as we have already stated, astronomical. Nor could a single accidental performance if it should happen establish any guarantee of its fixation and repetition. The last consideration is one to which the advocates of randomness have paid insufficient attention.

He urged the same argument also in relation to the larval symbiosis, as he called it, of the Large Blue caterpillar in the nest of the red ant, and to the perfection of the orb-web of the spider *Epeira diademata* (First Series, pp. 211–212 and footnote; Second Series, pp. 13–17), with the comment on Darwin:

This was of course repeatedly urged by critics like Asa Gray in Darwin's own lifetime. He never succeeded in answering it or even appreciating its character. His successors have not been much more successful.

Sir James Gray referred in a letter to *Nature* to the 'cheating' that would have to go on if evolution were to proceed by natural selection; and J.W.S. Pringle treated me with great hauteur for believing in natural selection; he had consulted his father-in-law (the Cambridge botanist H. Gilbert-Carter) who had assured him that no-one could explain leaf-shapes by selection — you could see all sorts growing happily together on any roadside.

Raven was answered by David Lack who pointed out the very various adaptations of different species of cuckoo, but never accepted Lack's arguments (Dillistone 1975, appendix 1). Lack, who migrated from Cam-

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bridge to Oxford, had convinced himself from his own studies of Darwin's finches, that their specific characters were truly adaptive, after starting with the opposite belief (see Provine 1986). He was the only religious man whom I knew at the period who did not allow his religion to dictate his view of natural selection. He took a great interest in our work on *Cepaea*. Elton was a very private man; I never knew what his religious or philosophical beliefs were.

Elton had a well-founded distrust of mathematical theorizers. Haldane (1932) had rejected his idea of the spread of neutral genes during population cycles, having calculated that random extinction could play only a 'very subordinate part in evolution, even in favourable cases'. Elton (1938), not inclined to give up a good idea for what might well be dubious reasons, replied:

The calculation may require revision in the light of the undoubted fact that reduction of numbers takes place patchily... [and there might be a local isolated refuge from which the mutant could spread]. This sort of process might not happen very often, but when it did, the result would perhaps be crucial... There is no way in which we can calculate the probability of this process taking place for a particular species or a particular mutation. The only way in which the matter can be carried further is to undertake marking experiments on various mixed populations on a large scale in the field, and follow their fate through several cycles of increase and decrease. Until this has been done, the matter cannot be considered as closed. The fact that mathematical calculations about field populations are at present limited very closely by their framework of assumptions, e.g. about random distribution, and that there are many irregular field phenomena that cannot be treated theoretically, is often forgotten.

Neither Robson (1928) nor Robson and Richards (1936, pp. 320–322) appear to have had any idea that, given a sufficient number of small fluctuating populations, a spread of neutral mutations would occur simply by chance in some of them. Elton himself (1930, pp. 79–82, duly noted by Robson and Richards 1936) recognized as a serious difficulty to his theory that only selection, apparently, could spread a gene, but did think it possible by chance, and worked out a numerical example. He even said explicitly that adaptations had two sources, by selection and by chance (p. 76). Professor W. B. Provine points out to me that the first exposition of a stochastic function in evolution was by Fisher in 1922; he dismissed it as merely generating unimportant noise in evolution. It must have been infuriating when Sewall Wright expanded the treatment in the 1930s and

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made it a major process in producing new gene combinations. Elton and Wright, so far as I know, do not mention each other before 1948, nor does Elton mention Fisher in 1927, 1930, 1933 or 1938.

When we turn to Ford in the 1930s his resemblance to Robson and Richards is at first startling. In the first edition of his *Mendelism and Evolution* (1931) we read:

The strong probability that the effects of the genes are multiple has already been discussed. This consideration may throw some light on the nature of the characters which separate local races and closely allied species. That these are sometimes entirely non-adaptive has been demonstrated, we believe successfully, by Richards and Robson (1926).

It is evident that certain genes which either initially or ultimately have beneficial effects may at the same time produce characters of a non-adaptive type which will therefore be established with them. Such characters may sometimes serve most easily to distinguish different races or species; indeed, they may be the only ones ordinarily available, when the advantages with which they are associated are of a physiological nature. Further, it may happen that the chain of reactions which a gene sets going is of advantage, while the end-product to which this gives rise, say a character in a juvenile or the adult stage, is of no adaptive significance. For this latter suggestion I am indebted to Mr. C.S. Elton.

J.S. Huxley (1924, 1927a and b) has pointed out another way in which non-adaptive specific differences may arise. For he has shown that changes in absolute body-size, in themselves probably adaptive, may automatically lead to disproportionate growth in a variety of structures, such as horns and antlers in Mammalia and the appendages in Arthropoda. The effects so produced may be very striking, but, as they are the inevitable result of alteration in size, they can rarely have an adaptive significance.

It is not perhaps always recognised how complete has been the demonstration provided by the above authors that the characters available to systematists for the separation of allied species may be of a wholly non-adaptive kind.

So far, then, Ford was as ready to recognize non-adaptive characters as Elton, no doubt partly from his own taxonomic experience, and quoted Richards and Robson in support. But he was well aware, and documents the phenomenon in his book, that mutants have effects on viability, as apparently did the unidentified genes responsible for the non-adaptive change in the wing pattern in the Marsh Fritillary. He continues, therefore:

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We are not justified, however, in assuming that they [the specific characters] have been established by a process of non-adaptive evolutionary change. Many of them are very invariable. An example is provided by the chitinous processes within the claspers of some male moths. These may show most constant differences in allied species; yet the female parts are often identical with each other and quite unmodified to fit those of the male, which therefore appear almost certainly to be non-adaptive. Yet it is gravely to be doubted if the uniformity of each male type could be preserved in the absence of at least associated stabilizing selection. Even if a non-adaptive character were to be established by chance survival, it appears to the author in the highest degree improbable that it could be maintained in a constant condition purely fortuitously.

Most of this quotation, except for the last few sentences, was preserved nearly intact in the 1939 and even 1954 editions of the book. Ford was right to notice the constancy of the genital armature, rather less critical in accepting the inevitability of allometric growth (it is itself a relationship selected for). What surprised me was that he never asked himself, nor did Elton, nor Robson and Richards, nor anyone else that I knew of, whether what they could see by simple looking was all that there was to a character. Fisher was no exception, being dependent on Ford for observation both in the field and in the collection. In 1931, quoting Ford, he remarked of the pleiotropic effect of a colour-pattern gene in a ladybird on the shape of the spermatheca, described by Dobzhansky, that:

...in the case of a small change in the proportions of an internal organ we have exceptionally good grounds for presuming the absence of selective action.

What was it, then, that led Ford, in contrast to Elton or Robson and Richards, to the belief that many characters might be in themselves non-adaptive, but the genes determining them and other, adaptive, characters were always under some selective influence? He was much impressed by, and often referred to, Fisher's mathematical demonstration (a field demonstration was out of the question) in *The Genetical Theory of Natural Selection* (1930, p. 80) that a neutral gene derived from a single mutation could only be in about the same number of individuals as there had been generations since its inception (Ford 1931, p. 81) and by Fisher's showing (1927) that for a polymorphism to be stable, there must be a balance of advantages and disadvantages. The disadvantage preventing fixation could be frequency-dependent, as was obvious in polymorphic mimicry when the mimetics became too common and attracted the predator; but it could