LETTERS TO THE EDITORS

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Animal Learning and Evolution

EVER since the original enunciation by Baldwin[1] in 1896 of the theory of 'organic selection', the suggestion that local differences of habit (local 'traditions' as Elton[2] has termed them) may be the starting point for the evolution of new species of animals has been from time to time put forward in various forms. Such habit 'traditions', if entirely of a phenotypic nature, can of course only exist in animals in which there is some ability and opportunity for perpetuation of a particular type of behaviour or attachment to a particular environment or locality by means of associative conditioning, imprinting, or some other type of learning. Many peculiarities of behaviour which appear to be of this kind are known to naturalists; particularly to those who study such subjects as host selection of phytophagous and parasitic insects or the local variation in behaviour of birds (for example, song, nest-site, feeding habits, etc.). Many examples will be found in recent publications (refs. 3–8). That they may be very constant and persistent is suggested by the fact that, in a number of cases, highly characteristic and constant behaviour patterns of birds (such as song type), usually regarded as typical examples of specific characters, are now known to be, in part at least, transmitted from generation to generation by learning.

But while the idea that certain differences of this kind may be of evolutionary significance has proved attractive to various writers, it has been difficult, without invoking some form of Lamarckism, to visualize the mechanism whereby behavioural differences characteristic of local populations could become genetically fixed. It is true that the Sewall Wright effect might be operative in small populations; but recent criticism by Mather[9] makes the probable significance of the Sewall Wright effect appear less; and in any event Wright's theory, while it might provide for random change, would not of itself favour the genetical fixation of variation of the same kind and *in the same direction* as the pre-existing behavioural trend based on learning.

Huxley suggests (ref. 6, p. 524) that the organic selection principle might be expected to account for the replacement of non-heritable variations by 'mutations' (presumably merely on account of the increased adaptation to the niche thus conferred), and that "where the modifications are extensive the process of their replacement by mutations may closely simulate lamarckism". The object of the present communication is to suggest that recent developments in genetics and in the field of animal learning, particularly the concept of imprinting due to Lorenz and others (refs. in Thorpe[4]), make the principle at once more probable and easier to understand.

Mather[9] has pointed out that the kinds of character which are likely to distinguish races and species are polygenic, and that any small decrease in mating freedom between two populations, whether brought about by natural obstacles or by any other cause, will be sufficient to lessen the intensity of selection for good 'relational balance'. The result of this will be that when members of two such populations or strains cross, the offspring will be heterotic. Mather further brings forward evidence to show that heterotic individuals are often less fit than the parental types, and that the avoidance of heterosis is probably the most widespread stimulant of isolating devices. Such a system, once started, would be self-propagating and irreversible.

Suppose for the sake of argument that the initial basis of separation is a host-plant preference based on olfactory conditioning, or a 'locality imprinting' holding the animal to a restricted locality or environment[4], renewed afresh in each generation. Suppose also that this is strong enough and has continued long enough significantly to reduce the intensity of selection for relational balance. There will thus be a definite selective advantage for such new variants as favour more complete isolation. Among new germinal variants of equal magnitude, those which are of the same nature and direction as the phenotypic learned response already operating will, besides resulting in closer adaptation to the niche, be the most effective in furthering isolation, and will therefore be most strongly favoured by natural selection. Thus the learned or conditioned response of the animal to the environmental situation will, besides tending to reinforce and make effective slight topographical and geographical barriers, give momentum to, and set the direction for, the selective processes tending to bring about genotypic isolation. These selective processes will thus bring about the reinforcement and perhaps the eventual replacement of non-heritable modifications by genetic modifications, and will thus closely simulate a Lamarckian effect.

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[2] Elton, C., "Animal Ecology and Evolution" (1930).
[3] Thorpe, W. H., "Ecology and the Future of Systematics" in "The New Systematics", ed. J. S. Huxley (1940).
[4] Thorpe, W. H., *Brit. J. Psychol.*, **34**, 66 (1944).
[5] Thorpe, W. H., *J. Animal Ecol.*, in the press (1945).
[6] Huxley, J. S., "Evolution: The Modern Synthesis" (1943).
[7] Mayr, E., "Systematics and the Origin of Species" (1942).
[8] Cushing, J. E., Jr., *Condor*, **46**, 265 (1944).
[9] Mather, K., *Biol. Rev.*, **18**, 32 (1943).

Inheritance of Melanism in Grey Squirrels

WHILE shooting grey squirrels on the Duke of Bedford's estate at Woburn this spring, some specimens were obtained which throw light on the inheritance of melanism in this species (*Sciurus carolinensis* Gmelin). So far as can be discovered, there is nothing in the literature about this. Nelson[1] states that in some parts of America litters are found to contain a black young; but there is no information on the proportion of black to grey young, or on the colour of the parents.

A grey male and female were shot in March of this year at Woburn, and a litter of four young taken from the drey which they had been occupying. Of these, one was black. If, as seems likely, the adults shot were the parents, they would appear to have been heterozygotes, carrying the factor for melanism, and it may be assumed that a proportion of the young of the normal grey colour were also heterozygotes; thus melanism in this species seems to be recessive and unifactorial.