will be brown. The negative correlation between the number of the day and β remains significant only at the 10 per cent level ($r = -0{\cdot}41$) after removing the influence of the number of baits taken using partial correlation. This indicates an increasing intensity of the searching image on successive visits. Although the data show reciprocal patterns in the trials with high brown frequency, none of the relevant correlations is significant at the 5 per cent level.

It is therefore unlikely that the results at the site with high green frequency are a consequence of the blackbirds having an initial preference for green baits. However, the results at the site with high brown frequency could be interpreted in terms of a preference for brown baits maintained through the experiment. It should be pointed out that results in experiments of this type may be influenced by changes in availability of prey outside the confines of the experiment. Any conclusions drawn must therefore be tentative.

3. Conclusions

We consider that these experiments indicate selection behaviour by blackbirds that would tend to maintain a rare colour morph in a prey population at extremely high density.

Acknowledgments.—We would like to thank Mr David Horsley for valuable comments on an earlier manuscript, and Dr C. R. Bantock and Mr R. D. Ward for critically reading this manuscript. We are also grateful to Professor E. W. Knight-Jones for facilities at Swansea.

4. References

ALLEN, J. A., AND CLARKE, B. 1968. Evidence for apostatic selection on the part of wild Passerines. *Nature*, *220*, 501-502.

ALLEN, J. A. 1972. Evidence for stabilising and apostatic selection by wild blackbirds. *Nature*, *237*, 348-349.

CLARKE, B. 1962. Balanced polymorphism and the diversity of sympatric species. In *Taxonomy and Geography*, ed. D. Nichols. Syst. Ass. Publ. 4, Oxford.

MANLY, B. F. J. 1973. Tables for the analysis of selective predation experiments. *Res. Popul. Ecol.*, *14*, 74-81.

The Munsell Book of Color. 1966. Munsell Color Co. Inc., Baltimore.

TINBERGEN, L. 1960. The natural control of insects in pinewoods. 1. Factors influencing the intensity of predation by songbirds. *Arch. Neer. Zool.*, *13*, 265-343.

THE DEFINITION OF THE TERM DISRUPTIVE SELECTION

ERNST MAYR

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02158

Received 4.xii.73

The term " disruptive selection " was introduced by Mather (1953). It is selection applied to the phenotypes of a variable population which " may favour both extremes simultaneously, though not necessarily to the same extent, at the expense of the average " (*loc. cit.*, p. 73). As a result it will convert an originally unimodal normal distribution into a bimodal distribution and in more extreme cases into two entirely separate distributions. The term " disruptive " in this terminology is unfortunate because, as Mather himself emphasised (*loc. cit.*, p. 70) " the forms in a polymorphic population are mutually adaptive; they do not represent the beginning of a break-up ". For this reason Dobzhansky has suggested the term " diversifying evolution " for this phenomenon (Dobzhansky, 1970).

Recently, however, Thoday (1972), has revived the term disruptive selection in a sense quite different from the one originally given by Mather: " Disruptive selection is selection for more than one value, that is selection which, within any one generation, favours different phenotypes *in different parts of an interbreeding population* " (italics mine). If we look at this definition we notice that the italicised words introduce qualifications which were not part of Mather's original concept. The phenomenon, to which Mather gave the term " disruptive selection ", had been known long before Mather and had been used by R. A. Fisher to explain the origin of polymorphism, sexual dimorphism, etc. In no instance was there any reference to " different parts of the . . . population ", by which Thoday understands geographic variation, as is apparent from his ensuing discussion.

With the help of this changed definition Thoday applies the term " disruptive selection " to all sorts of phenomena which previously had been referred to either as directive selection or as stabilising selection (the elimination of pheno-deviants). This expanded application is, in part, a result of his interpretation of the term " interbreeding population ". As originally conceived by R. A. Fisher and Mather the " population " in which disruptive selection occurred was at the same time the population as conceived by the statistician as well as the local " effective breeding population ". Thoday now extends the term, with an unfortunate loss of precision, to the totality of interbreeding populations, for instance the biological species as a whole. Selection against hybrids, one of the classical illustrations of stabilising selection, is now included by him under " disruptive selection ": " Every hybrid zone which is not expanding, and every case where hybrids are formed in nature but are inviable or sterile, provides an example where disruptive selection is maintaining species differences " (Thoday, 1972, p. 136). Nothing is gained and just about everything lost by transferring the term " disruptive selection " from the phenomenon for which it had originally been coined and to which it has been traditionally applied, to a phenomenon which is traditionally called stabilising selection.

Thoday now applies the term also to directive selection. In species of plants which are able to live on the toxic tailings of a lead or zinc mine, a local population may evolve which is selected for a high degree of resistance to these toxic effects. Populations of the same species which occur outside the poisoned area remain unchanged. This is a typical case of spatial variation, in principle a case of geographic variation on a local scale because, in spite of some gene flow, the plants outside the tailings form a different population from those growing on the toxic soil. It is a textbook illustration of directive selection. If Thoday now refers to this as disruptive selection, he thoroughly confuses his readers.

He goes further than that and refers to numerous cases of reinforcement of isolating mechanisms in zones of overlap of partially sympatric species as disruptive selection. These are, of course, characteristic examples of the phenomenon to which Darwin had referred as " character divergence ", illustrating directive selection. [I might add parenthetically that great confusion would be avoided if the term " reinforcement of isolating mechanisms " were used in all cases in which isolating mechanisms are involved, and Brown and Wilson's (1956) term " character displacement " for all components that deal with competition, that is with niche occupation.]

There is no need for a discussion of the conclusions which Thoday derives from his new definitions because there is little argument as soon as one replaces his new terminology with the traditional ones. Thoday's discussion, however, is a graphic illustration of the potential danger of confusion which arises when an author replaces a traditional terminology by one which up to that time had been used for an entirely different set of phenomena. A clear distinction must be made in evolutionary discussions between geographic variation (including ecotypic selection), isolation, stabilising selection, reinforcement of isolating mechanisms, character displacement (owing to interspecies competition), and disruptive (or better: diversifying) selection. Only confusion can result from an intermingling of these very different evolutionary phenomena under the same terms.

References

BROWN, W. L., AND WILSON, E.O. 1956. Character displacement. *Syst. Zool.*, *5*, 49-64.

DOBZHANSKY, TH. 1970. *Genetics of the Evolutionary Process*, pp. 167-172. Columbia University Press, New York. 505 p.

MATHER, K. 1953. The genetical structure of populations, pp. 66-95. In *Symposia Soc. Exp. Biol.*, vol. VIII.

THODAY, J. M. 1972. Disruptive selection. *Proc. R. Soc. London, B*, *182*, 109-143.

DEFINITIONS OF DISRUPTIVE SELECTION AND OF " INTERBREEDING POPULATIONS "

J. M. THODAY

Department of Genetics, University of Cambridge

Received 20.xii.73

I AM glad that Mayr (1974) has questioned the definition of " disruptive selection " for it brings out the very real problems which I (1972) had to face in trying to discuss the experimental results and their possible relevance to nature. The problems arise, of course, because the concept " interbreeding population " is abstract and there are consequential difficulties of deciding, except, as I put it, for " model builders and designers of laboratory experiments " when we are dealing with one " interbreeding population " and when we are dealing with more than one.

Even in the conduct of experiments there are difficulties for under certain conditions of selection and mating system, given appropriate genetic variance, selection can, during the course of a single experiment, convert one population into what might be regarded in at least some senses as two.

Fisher (1930) discussed a particular effect of disruptive selection (though he called it stabilising selection, presumably because the effect was to