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.

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DEFINITIONS OF DISRUPTIVE SELECTION AND OF " INTERBREEDING POPULATIONS "

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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

stabilise intermediate gene frequencies). Simpson (1944) used the term centrifugal selection, a term that he applied both to the situation when differing parts of what was originally one population exchange genes and to the situation when they do not. Mather (1953, p. 84) refers to " sub-populations " and in his main paper on the subject (1955) clearly considered disruptive selection a term that applies to a situation in which one population is also two subpopulations. To quote: " Disruptive selection arises when several optima are favoured." " . . . disruptive selection, if it is effective, must result in that adjusted discontinuity at the phenotypic level which is a feature of both isolation and polymorphism. In the case of isolation, however, this is accompanied by disruption of the erstwhile common gene pool, whereas in polymorphism the morphic types continue to share a common gene pool (apart from any switch genes that may be involved) . . .". Given three conditions, that " the optimal phenotypes must be independent ", that " genetic exchange between the populations " must " not rise above a certain maximum ", and that " the difference in environment . . . must be persistent (which must in general require spatial separation of the groups) genetic isolation . . . will be the outcome of disruptive selection ".

I do not think my definition differs from Mather's. If selection favours several optima, the population must have parts in which the different optima are favoured, for an *individual* cannot be exposed to selection for antithetic optima. I treated disruptive selection as broadly as I did because my experience in experiment enforced my realisation that the term " popula-tion " is quite imprecise except in theory, and that this imprecision is at the heart of many of our difficulties in natural population and evolutionary genetics. Ask the question of any natural situation: " Am I dealing with one population or more? ", and the answer has to be " It depends upon the amount of gene exchange between the parts ". Now it is clear that if the parts under consideration are the two sexes of a mating pair they each belong to the other's population (though this does not help us to define the population to which the mating pair itself belongs). This is the extreme situation of the kind Mather (1955) referred to as interdependence where " the various phenotypes favoured by selection are bound together in function ". When they are not so bound, however, as when the members of a species in an area are selected differentially through heterogeneity of habitat, then answers to the questions whether we have one population or more will depend on the gene exchange occurring and the way we look at the problem.

Take for example the lead mine populations studied by Bradshaw and his colleagues which Mayr regards as " a textbook illustration of directive selection ", but to which Bradshaw clearly thought disruptive selection was relevant. It is of course possible to look at the individuals on the lead mine and say this we shall define as one population into and out of which genes are flowing by migration, and to describe that population as being directionally selected for lead resistance. Then we have to consider the members of the species adjacent to but outside the poisoned area as a different population exposed to the opposite type of gene flow and a different direction of selection. But if we do this we have in effect defined away the problem that gives interest to the particular populations, which is how the differences between the two subpopulations originated and are maintained against the homogenising effects of gene flow of considerable magnitude. If our interest

is in this problem then we must regard the two subpopulations as parts of one larger population.

We could of course make entirely arbitrary decisions concerning the maximum amount of gene flow required for two sets of individuals to be defined as two populations, but unless we are prepared to do this we must recognise that we are not dealing with a strictly definable concept (except in theory) when we talk of a natural population, and, if we do do it we must measure the gene flow directly before we can define our populations.

Again, Mayr regards selection against hybrids as a classical example of stabilising selection. If one looks at only one of the entities that are hybridising, then the hybrids are deviants being eliminated and this could perhaps be thought of as stabilising selection, though not I think in some of the senses in which that term has been used, *e.g.* Mather's (1953) sense. But if one considers both the entities that are involved, the matter again involves quantities not qualities. How much hybridisation is required, and how fertile or viable are the hybrids to be before one must talk of the two parts of a population instead of two separate populations?

These points may help to make clear why I treated all the phenomena I did as involving disruptive selection. It is the concept " population " that lacks precision (except in theoretical studies). There is a continuum of concepts of population. At one end there is the purely sympatric group of individuals interbreeding at random and completely isolated from all other individuals. Then there are clinical or mosaic series of partially isolated subpopulations exchanging (by random or selective migration which may may have opposite consequences) genes in frequencies from anything slightly less than that implied by random mating downwards. At the other end there is the situation where some set of such subpopulations exchanges so few genes with another set that drift is more important as a cause of divergence than is migration (if random) as a cause of convergence. I think that it would be more confusing to introduce artificial boundaries in this continuum than to use the term disruptive selection consistently throughout, especially as it draws attention to the danger of using an imprecise term " population " as if we were able to apply it precisely.

In truth " What is a population? " is not the right question. " What is the population structure of a species? " is, which is why breeding system, breeding structure, inbreeding, outbreeding, assortative mating, gene-migration, both random and selective, and both zygotic and gametic, habitat choice, and partial isolation are such important concepts though they overlap in meaning. We cannot define a population in such a way that the population of which a particular individual is a member includes only individuals that are members of that population alone, unless we mean a set of individuals *completely* isolated from any other. When we talk of *a* population we either mean something in abstract theory, or a laboratory isolate, or those individuals in the place we are studying, or some partial isolate, some of the individuals in which also belong to different partial isolates. Two sets of individuals that are partially isolated are each separate populations and are together one population. If we try to define *a* population so that an individual can only belong to one population we can only confuse ourselves and will never understand nature.

If I have thoroughly confused my readers by applying the term " disruptive selection " in the only way I can see it can be applied, perhaps it

implies confusion about what natural populations are. All the phenomena I discussed in my review (except in the extreme examples where hybrids are completely sterile) involve sets of individuals selected for different properties but exchanging genes to some extent. To the extent that they exchange genes they must be regarded as parts of one interbreeding population under disruptive selection.

Finally I think that Mather's use of " disruptive " to describe this type of selection is justifiable. Disrupting the population is precisely what it " tries " to do. What prevents it from doing so, in the conditions in which it leads instead to polymorphism, is not a matter of the kind of selection. It fails to disrupt (that is to split) the population if its intensity or persistence is inadequate, if the necessary genetic variance is not available, or if the breeding system holds the parts of the population together. The various laboratory experiments that have been done using disruptive selection have had very different results. The differences do not depend on differences of the type of selection, but on the mating systems used, that is on the population stucture imposed or allowed to develop. It would be wrong so to define disruptive selection that the definition depended more on the breeding structure than on the selection itself.

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A GENE INVOLVED IN LYSINE EXCRETION IN *ESCHERICHIA COLI* K12

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Summary

One of our laboratory strains of *Escherichia coli* K12 carries an allele, *lysX*, which permits the excretion of lysine. Other strains do not carry this allele. The *lysX* gene maps on the side of *argA* distal to *thyA*, at about 53·5 minutes. In partial diploids the *lysX* allele is recessive to the *lysX+* (non-excretor) allele.

1. Introduction

MUTANTS of *Escherichia coli* have frequently been observed to overproduce and excrete normal metabolites. In a series of transduction experiments

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