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REVIEW LECTURE

Disruptive selection

BY J. M. THODAY, F.R.S.
University of Cambridge, Department of Genetics, Milton Road, Cambridge, CB4 1XH

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A population is exposed to disruptive selection if more than one phenotype has optimal fitness and intermediate phenotypes have lower fitnesses. Maintenance of the two or more optima may depend upon their relative fitnesses being frequency dependent. Such selection may be expected in two contrasting types of situation. First the two or more optimal phenotypes may depend on one another as do the two sexes in a bisexual species. Secondly the optima may be set by heterogeneity of the environment. Then we may think in terms of a mosaic of ecological niches or a clinal situation, and may expect that gene flow will tend to promote convergence of the sub-populations while disruptive selection tends to promote their divergence. Disruptive selection may therefore be relevant both to the evolution and maintenance of polymorphisms and to the divergence of parts of populations one from another, under the influence of variation of ecological conditions within the range of gametic and/or zygotic dispersal.

Disruptive selection has been shown to be capable of increasing phenotypic and genetic variance, of producing and maintaining polymorphisms, of causing divergence of sub-populations between which substantial gene exchange occurs, and of splitting a population into two which are genetically isolated from one another. These results are reviewed and their relevance to natural populations discussed.

I. INTRODUCTION

I 1. *Definitions of disruptive selection*

Selection (figure 1) whether natural or artificial, may be classified into three main types, directional, stabilizing and disruptive, to use the terms of Mather (1953). Directional selection is selection in one direction away from the mean. Stabilizing selection is selection for some intermediate value and against deviation from that value in either direction. Disruptive selection is selection for more than one value, that is selection which, within any one generation, favours different phenotypes in differents parts of an interbreeding population.

This definition of disruptive selection gives difficulty in only one respect. This difficulty arises because it is possible in principle, and, as we shall see, in experiment, for disruptive selection gradually to divide a population into two populations between which there is decreasing gene exchange. When this process is complete, disruptive selection becomes directional selection. Selection is however to be defined as disruptive so long as some hybrids between the different parts of the population are formed and have to be eliminated by that selection. If no hybrids are formed we have two or more populations under what I will call divergent directional selection (Thoday 1959). Simpson's 'centrifugal' selection includes divergent directional selection (see Simpson 1944, p. 84).

Disruptive selection as defined here might be expected to occur:

(i) Where heterogeneity of selection is intrinsic to the biology of the population itself as with sex dimorphism, heterostyly, sex-limited polymorphism, and any form of genetic facilitation, that is cooperation between genotypes.

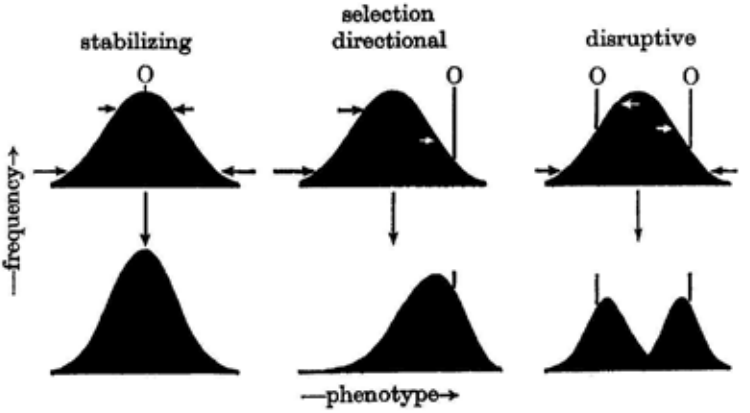

FIGURE 1. The three basic types of selection. The optimum expressions of the phenotype are indicated by O, and the directions and relative magnitudes of the selective forces by the horizontal arrows. Selection is heavier against phenotypes farther away from the optimum (after Mather 1953).

(ii) Where heterogeneity of selection arises from environmental heterogeneity in space, either because there is a mosaic of differing ecological niches which the population may occupy, or because there is linear variation of some relevant environmental factor such as may be the cause of some phenotype frequency clines. These two both reduce in simplest form to a model situation that applies to most published experiments. It can be imagined in terms of two adjacent environments differing in biologically significant factors, at least one of which is within the range of gametic and/or zygotic dispersal from the other. These may then be regarded as a small section of a more extended linear environmental change in space, or as two components of a mosaic environment.

12. *General considerations in the design of disruptive selection experiments*

Disruptive selection experiments fitting this model have been done in various ways, differing with the mating systems employed, the quantity and kind of gene migration between the selected classes, the complexity of the selection system, and with the complexity of the environment.

Disruptive selection with respect to phenotype may be *symmetrical*, where equal numbers of individuals are chosen from two separate points of the distribution. If these are not the two ends of the distribution there is also stabilizing selection around two values. On the other hand disruptive selection might be *asymmetrical*

where two parts of the distribution are favoured but more of one than of the other is chosen. Such selection clearly involves a directional as well as the disruptive element.

Important variables are the mating system, and the amount, direction and kind of gene flow. Disruptive selection may be carried out with negative or positive assortative or random mating. Migration may be random or selective. Mating may be *forced* by the experimenter, or *mating choice* may be allowed to the organisms, a point that is of vital importance. If the mating system is forced, the two (or more) classes of selected individuals may be made interdependent. If mating choice is allowed, gene flow will depend on the matings that happen, so that the different classes selected are allowed to become independent if they can. Mather (1955) discussed the importance of such interdependence or independence.

Whether or no the selected groups are allowed to compete for environmental resources is also important. If they are not, the disruptive selection may be occurring in a situation analogous to that which will occur with habitat selection in nature.

The remaining variable concerns the environment. We may design experiments specifically to test reaction to chosen environmental variables, or we may keep the environment as uniform as laboratory culture conditions permit. Specific environmental variables may be used when it is desired to test whether disruptive selection can affect environmental variance or genotype-environment interaction, that is to say, in developmental terms, the reactivity of the developmental system to the chosen environmental variables. Alternatively the use of specific environmental variables allows us to do laboratory experiments with natural rather than artificial disruptive selection.

13. *Disruptive selection and cyclic selection*

Mather (1955), and Thoday (1956, 1958, 1959) briefly discussed cyclic selection and its relation to disruptive selection. They both considered that the two might have something in common, but this is a matter that presents some difficulties.

We may define purely cyclic selection as occurring when different generations are exposed to different selective conditions such that genotypes that are the more fit in one generation are the less fit in another generation. Haldane & Jayakar (1963) have shown that such cyclic selection will only lead to stable intermediate gene frequencies if the fitness of heterozygotes averaged over the cycle is greater than that of either homozygote, and Beardmore (1966) has shown that cyclic selection in the absence of such heterozygous advantage leads to quite rapid fixation. We should therefore avoid confusing cyclic selection with disruptive selection.

Temporal cycles of environmental conditions may however give rise to disruptive selection in some circumstances, and spatial variation of the environment may impose some element of cyclic selection. Disruptive selection would arise in a cyclic environment, if, for example, there were overlapping generations. Then

part of a population may be selected so that the young fit one phase of the cycle and the adults fit another. Other parts of the population would be selected in the opposite sense. If this were at all consistent over the generations the population would consist of more or less separate parts selected for different properties. Some measure of cyclic selection will always arise from spatial heterogeneity especially with sessile plants, for some of the progeny of individuals selected in one part of the environment will be dispersed to a place where the environment differs, and some of their progeny in turn will fall in the environmental conditions in which the grandparents were selected.

Cyclic and disruptive selection, therefore, may often be confounded in nature. The matter will be complex, however, for the effects of an environmental cycle in time will depend greatly on the biology of the organisms under consideration, especially with respect to the extent of dispersal, to the amount of generation overlap and to the relation between the timings of any environmental cycle and the length of a generation (see Thoday 1964).

II. Results of laboratory experiments

II 1. *Disruptive selection and genetic diversity*

The earliest disruptive selection experiment to be published was made with forced negative assortative mating by Falconer & Robertson (1956) using weight of mice as a character. Thirteen generations of selection produced equivocal results, for, though the phenotypic variance of their disruptive line was greater than that of their stabilizing selection line, there was doubt concerning the cause of this difference. The mean of the disruptive selection line was the higher and no genetical analysis was attempted, so that it was not possible to say whether the results were merely consequences of a relation between variance and mean on an arithmetic scale. Similarly equivocal results of disruptive selection with negative assortative mating were published by Thoday (1958, 1959) using sternopleural chaeta number in *Drosophila melanogaster*. However, Thoday (1958, 1959) and Thoday & Boam (1959) obtained clear effects with a positive assortative mating system. The disruptive selection practised was symmetrical and the forced gene flow was maximal. The disruptive selection line clearly had greater phenotypic variance than the stock from which it came, though their means were similar. Much of the increase of phenotypic variance was a consequence of increased genetic variation (Thoday 1959; Thoday & Boam 1959; Gibson & Thoday 1962*a*, *b*; Wolstenholme & Thoday 1963).

Most experiments discussed below in different contexts, and many others, have shown that genetic diversity can be maintained or increased by disruptive selection. They include experiments with negative assortative mating, random mating, and mating choice, and with various amounts of random or selective migration. Some are symmetrical, some, for example those of Streams & Pimentel (1961) and Dobzhansky & Spassky (1967), involve extreme asymmetry of selection or of

migration. A few involve natural not artificial selection. Many involve sternopleural chaeta number in *Drosophila*, but other characters and organisms have been used. They include modification of expression of a wing vein mutant (Scharloo 1964, 1970*a*,*b*) EDTA toler ance (Robertson 1966), developmental rate (Prout 1962; Tigerstedt 1969), pupation site (de Souza, da Cunha & dos Santos 1970), body size

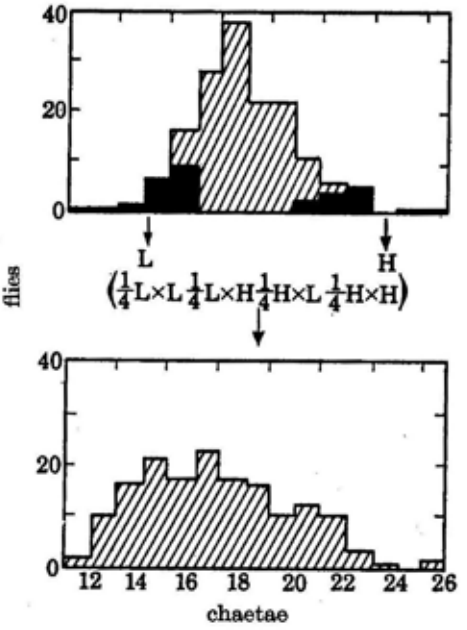

FIGURE 2. Increase of variance as a result of disruptive selection. The upper figure shows the distribution of sternopleural chaeta number in a newly captured population (Southacre) of *Drosophila melanogaster*. The lower figure shows the distribution after two generations of disruptive selection with quasi-random (see p. 122) mating. The 12.5 % with most and the 12.5 % with fewest chaeta were selected (black area) and these were mated in the four possible ways, H × H, H × L, L × H, L × L. Equal numbers of progeny from each mating were scored to give the progeny distribution.

(Bos 1969), escape behaviour (Grant & Mettler 1969), wing length (Tantawy & Tayel 1970), geotaxis and phototaxis (Dobzhansky & Spassky 1967; Dobzhansky, Spassy & Sved 1969; Dobzhansky, Levene & Spassky 1972), inversion frequency (Thomson 1964) and protein polymorphisms (Powell 1971) in *Drosophila*; pupal weight in *Tribolium* (Crenshaw 1966), and flowering time in maize (Paterniani 1969) and *Brassica* (Murty & Sharma, in press).

Figure 2 shows the results from this point of view of two generations of selection with quasi-random mating for sternopleural chaeta number taken from the data of Gibson & Thoday (1963).

All these results taken together indicate that a general effect of disruptive selection is to maintain and even promote genetic diversity within populations. This is consonant with numerous models which show that it is theoretically possible

for heterogeneous selective forces to maintain genetic heterogeneity through clinal selection or selection in different environmental niches (see, e.g., Fisher 1930, 1950; Haldane 1948; Levene 1953; Deakin 1955; Dempster 1956; Li 1955; Moran 1959; Levins 1965; Levins & MacArthur 1966; Hanson 1966; Smith 1966, 1970; Prout 1968; Bryant 1969; Cannings 1971; Bulmer 1971. See also Beardmore (1966) for computer simulation results).

The most interesting of these demonstrations that disruptive selection maintains genetic diversity has recently been published by Powell (1971). He set up 13 populations of *Drosophila willistoni* in laboratory cages. Each was started with 500 flies from the same Brazilian stock. Some cages were provided with only one kind of medium and one kind of yeast. Others had either different media or different yeasts in different vials, or else temperature was changed each week from 19 to 25 °C. In yet others both yeast and medium were varied and temperature was changed each week as well. After about a year the amount of variation was assessed at twenty-two enzyme loci. The constant environment populations averaged 7.8 % heterozygosity per individual. The populations given one environmental variable, medium, yeast or temperature, averaged 9.6 % heterozygosity. The populations with the three environmental variables averaged 13.4 %. The errors are of the order of ± 1 %, showing that more varied environments maintained a greater variety of alleles of this kind in the populations.

II 2. *Disruptive selection and polymorphism*

Disruptive selection can, however, have much more striking effects than these as Mather (1955) predicted. The genetic diversity it produces has sometimes resulted in quite complex polymorphism (Thoday & Boam 1959; Thoday 1960; Millicent & Thoday 1960, 1961; Gibson & Thoday 1959, 1962*a*,*b*; Wolstenholme & Thoday 1963; Scharloo, Hoogmoed & Ter Kuile 1967*b*; Barker & Cummins 1969; Wallace 1968; Scharloo 1970*a*,*b*; de Souza *et al.* 1970). I will only discuss here two of our polymorphisms that have been subjected to most revealing genetic analysis, and describe two others that also have special significance.

The first (Thoday & Boam 1959) was established by symmetrical disruptive selection with positive assortative mating from a wild stock (Dronfield) which derived from a single female *Drosophila melanogaster* captured near Sheffield. The variable was sternopleural chaeta number. The polymorphism, once established, was maintained as indicated in figure 3, four chaeta number loci being involved. The polymorphism was dual, and the population was trimorphic, chromosomes II and III each having a testcross system so that there were three phenotypic classes of fly selected in each generation, one High, one Low and the other intermediate in chaeta number. It was the intermediate flies that migrated from one half of the population to the other.

Genetically the chromosome III system is the simpler (Wolstenholme & Thoday 1963). There are two closely linked loci at 51 and 53 centimorgans on the standard map. The high chaeta number allele at each locus is fully dominant and adds 1.2

chaeta to the mean. There is no detectable interaction between loci. We cannot be certain how this chromosome III polymorphism originated for the high alleles were not identified in the Dronfield stock. It is, however, clear that disruptive selection not only maintained heterozygosity at these loci but also maintained the coupling linkage phase against some recombination pressure.

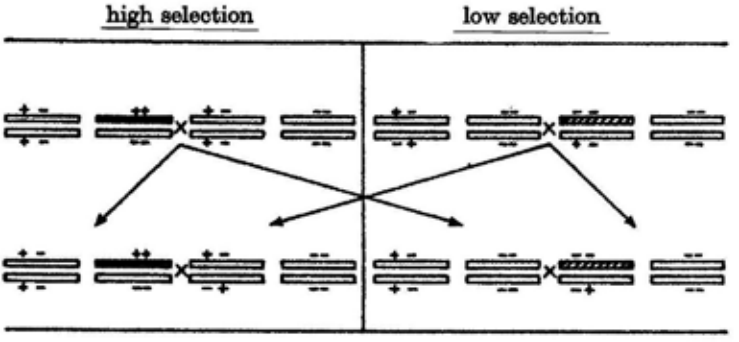

FIGURE 3. The polymorphism established by disruptive selection by Thoday & Boam (1959). The figure shows the genetics of the polymorphism. The mating system under which it was developed is given in table 1. The black third chromosome remains on the high side of the population and only its white homologue occurs in flies selected for low chaeta number as migrants to the low side. Likewise the hatched second chromosome is retained in the low half of the population. For details see text (from Thoday 1965).

The chromosome II loci are at about 27 and 47 centimorgans and have proved of great interest. Gibson & Thoday (1962*a*, *b*) were able to show that the extreme chromosome combining the low chaeta number alleles at both loci was lethal when homozygous, that the reciprocal recombinant was dominant lethal, and that the coupling heterozygote was also lethal. The repulsion heterozygote is perfectly viable and almost certainly heterotic so that we appear to have found a lethal cis-trans type position effect despite the two loci being 20 centimorgans apart.

The origin of this chromosome II polymorphism is understood for we demonstrated that the wild stock Dronfield with which we began the disruptive selection experiment was itself cryptically polymorphic and that the origin of the extreme low chaeta number chromosome depended on recombination. The wild stock contained both the repulsion chromosomes, $-+$ being the rarer.

The second polymorphism (Thoday 1960) was established by symmetrical disruptive selection with negative assortative mating in a population initiated from the F_2 of a cross between a very high chaeta number *vg*/*vg* selection line (vg 6 of Thoday & Boam 1961*a*) and a low chaeta number stock containing the marker genes *se*, *cp* and *e*. We later did considerable work locating the chaeta number genes in the parental stocks (Thoday, Gibson & Spickett 1964; Spickett & Thoday 1966; Wolstenholme & Thoday 1963). This, in conjunction with the evidence

provided by the marker genes in the line itself showed that the polymorphism was maintained by the genetic system given in figure 4.

Two features of this polymorphism are of great interest. First it further illustrates the extent to which disruptive selection is able to maintain non-random linkage phases against recombination pressure. In the original paper evidence was given showing how large this recombination pressure was. Second the system is a model example of what Fisher (1930) proposed must be involved in sexual dimorphism, incompatibility and complex polymorphisms in general. (See also Darlington & Mather 1949; Ford 1964; Sheppard 1969.) A heterozygous linked complex provides a segregational switching 'supergene' determining two developmental pathways just as the XY segregation does in sex dimorphism or the complex S locus does for

FIGURE 4. A polymorphism maintained by disruptive selection with negative assortative mating. There is a three locus segregational switch on chromosome III where + represents a chaeta-number increasing allele. The 'e' gene homozygous on chromosome II enhances the effects of this switch. There probably were other enhancers on chromosome I (after Thoday 1965).

heterostyly in *Primula*. Homozygous modifiers, here represented by the chromosome II gene and, we believe, others on chromosome I, affect the consequences of that switch, as is also so in sex dimorphism, heterostyly (Mather 1950) and in other polymorphisms such as those concerned with Batesian mimicry in *Papilio dardanus* that have been analysed so profitably by Clarke & Sheppard (1960). The design of our experiment, since selection was always within the progeny of single females, ensured that there could be no significant selection for reduced recombination within the supergene. Similar experiments with suitably modified design could test whether reduction of recombination within such supergenes readily occurs, as Fisher, Darlington and Sheppard have predicted.

Another striking segregational polymorphism has been established in the laboratory by *natural* disruptive selection: de Souza *et al.* (1970) have shown that populations of *Drosophila willistoni* in laboratory population cages develop behavioural dimorphism. The flies of new wild stocks only survive if they pupate in the cage vials. After a time new genotypes establish which pupate outside the vials so that thereafter two genotypes differing in pupation site are maintained and a larger population results. These experiments demonstrate that natural selection can rapidly produce polymorphism if a population is presented with a heterogeneous habitat.

These are segregational polymorphisms. It is however clear, as Mather (1955) pointed out, that an appropriate alternative response is for a population to produce

a genotype that is developmentally reactive to some factor that varies in the environment. Scharloo has obtained such a result using modification of cubitus interruptus expression in *Drosophila*. In one of his experiments (1970*a*) he used a mating choice system and obtained a segregational polymorphism with some dominance. In another (1970*b*) he used a negative assortative mating system and obtained a bimodal distribution that was partly determined by environmental variation. We may therefore conclude that disruptive selection may be responsible for the evolution of some epigenetic as well as segregational polymorphisms.

II 3. *Gene flow and divergence under disruptive selection*

Other results have undermined the concept that genetic differences between two populations must be 'swamped' in the absence of isolating factors. This had at one time become almost a textbook dogma, but our earliest experiment, published in 1959, showed that it was not true. Though older, the concept took its justification from the mathematical theories of panmixis and of *random* migration. But there were always three objections that could be made to it. First, it had never been put to adequate experimental test, for no experimental measures had been made of the relationship between selection, gene migration and divergence. Second, it involves a confusion of random mating with respect to zygotic genotype frequencies and random mating with respect to adult genotype frequencies, and is not true unless gene migration between two sub-populations is sufficient to counter-balance any differential selection between them. Third, if migration is selective, the selective migration of itself can be a powerful force leading to divergence (see Fisher 1930; Edwards 1963; Parsons 1963; Kempton 1971 for theory; Thoday & Gibson 1970*b* for experimental evidence).

The first relevant experiment was published by Thoday & Boam in 1959 using 50% gene flow. Details of the maintenance of this line were given in the original publications (Thoday 1959; Thoday & Boam 1959). It is only necessary to reiterate here that each generation was represented by four single-pair cultures, two of which were selected for high and two for low sternopleural chaeta number. Twenty flies of each sex from each culture were assayed and one fly was selected from each 20. The mating system is described in table 1. There were two high male-lines and two low male-lines. Each selected high male was mated in each generation to a female selected for high chaeta-number but taken from a culture of a low male-line. Likewise a low male was mated to a low female from a culture of a high male-line.

There were therefore in each generation two high and two low cultures, but cross-mating ensured that they were all parts of the same population, which was subjected in every generation to selection for both extreme chaeta-numbers.

This population can be considered in terms of its component high and low sub-populations. These were not isolated in any way. On the contrary all flies were progeny of crosses between the two sub-populations, the migration being selective.

The difference between the mean chaeta-numbers of the two high cultures and

that of the two low cultures (figure 5) fluctuated widely at first, sometimes having negative values, but after generation 13 the population was able to maintain a consistent and increasing positive difference between its high and low components.

TABLE 1. THODAY & BOAM'S MATING SYSTEM

	culture: i.e. male sub-line			
parents of	1 (H)	2 (H)	3 (L)	4 (L)
generation	♀ ♂	♀ ♂	♀ ♂	♀ ♂
n	H3 × H1	H4 × H2	L1 × L3	L2 × L4
$n+1$	H4 × H1	H3 × H2	L2 × L3	L1 × L4
$n+2$	H3 × H1	H4 × H2	L1 × L3	L2 × L4
$n+3$	H4 × H1	H3 × H2	L2 × L3	L1 × L4

The entries designate the flies used to produce the culture in the generation shown in the first column. H indicates the highest and L the lowest chaeta-number fly found in the appropriate culture. 1, 2, 3, 4 indicate the culture from which the fly was taken.

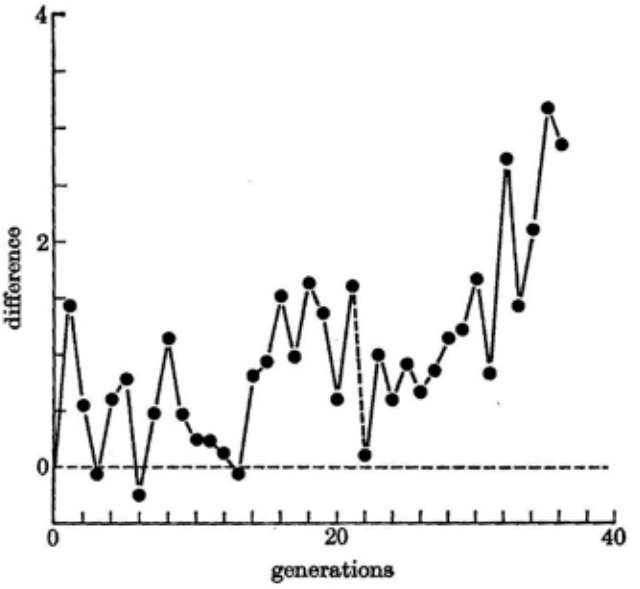

FIGURE 5. Divergence under disruptive selection with 50 % gene flow. The figure shows the mean difference of chaeta-number between the selected high and low halves of Thoday & Boam's (1959) population (after Thoday & Boam 1959).

Since the gene flow between the two halves of this population was maximal, that is twice as much as would occur with random mating, these results left no doubt that isolation is not a prerequisite of divergence. This divergence was maintained as a genetic polymorphism, the details of which have already been described above (figure 3).

Following this, Millicent & Thoday (1960, 1961) did experiments of essentially the same kind with the same base population (Dronfield), but using mating systems

that gave 50 %, 25 % and 0 % gene flow. The mating systems are given in table 2. 0 % gene-flow is of course divergent directional selection. 25 % gene flow is the equivalent of that which is expected with random mating since the selection was symmetrical. The two permit us to compare divergence under conditions involving the minimum and what is (except when there are the special relations between the two selected classes that we see in sexual dimorphism) the maximum mean two way gene flow likely in nature. The results are reproduced in figure 6. Divergence under 50 % gene flow occurred but was less striking than in Thoday & Boam's (1959) experiment. Divergence under 25 % gene flow was slower but ultimately of the same order of magnitude as that with complete isolation.

TABLE 2. THE MATING AND SELECTION SCHEMES GIVING 50 % AND 25 % AND 0 % GENE EXCHANGE

			♂ parent in generation			
population	culture	♀ parent	1	2	3	4 etc.
50 % gene-exchange	A	AH	CH	DH	CH	DH
	B	BH	DH	CH	DH	CH
	C	CL	AL	BL	AL	BL
	D	DL	BL	AL	BL	AL
25 % gene-exchange	A	AH	BH	DH	BH	DH
	B	BH	CH	AH	CH	AH
	C	CL	DL	BL	DL	BL
	D	DL	AL	CL	AL	CL
0 % gene-exchange	A	AH	BH	BH	BH	BH
	B	BH	AH	AH	AH	AH
	C	CL	DL	DL	DL	DL
	D	DL	CL	CL	CL	CL

H indicates the highest, and L the lowest flies chosen from a sample of twenty. The letters A–D indicate the female sub-line from which the designated flies are taken. Only males are chosen to migrate.

The 'positive assortative mating' system of these 25 % gene flow populations was clearly a factor favouring divergence, for the migrants from the high to the low side of the population were selected for low chaeta number and those migrating in the opposite direction were selected for high chaeta number. Migration was selective and the system is therefore one analogous to habitat selection. To test whether this was essential if divergence was to be maintained, one of the 25 % gene flow lines was put under the opposite regime, in which migrants were selected in the same way as non-migrants. This first reduced the difference between the progenies, but it rapidly recovered (figure 6) showing that disruptive selection can maintain divergence under these conditions.

It is important that we be clear about these two types of migration. The first, which we will call positively selective migration, is analogous to habitat selection when migrants move from unfavourable to favourable environments according to their genotypes. The second, negatively selective migration, is as unfavourable to

divergence as it can be, for the migrant flies move genes away from the sub-population in which those genes are favoured. That divergence was maintained despite this extremely unfavourable form of selective migration is striking evidence that dependence of divergence on isolation has been greatly exaggerated.

Gibson & Thoday (in press) have since compared these systems and shown that disruptive selection with 25 % negatively selective migration is able to promote as well as maintain divergence. The results are summarized in figure 7.

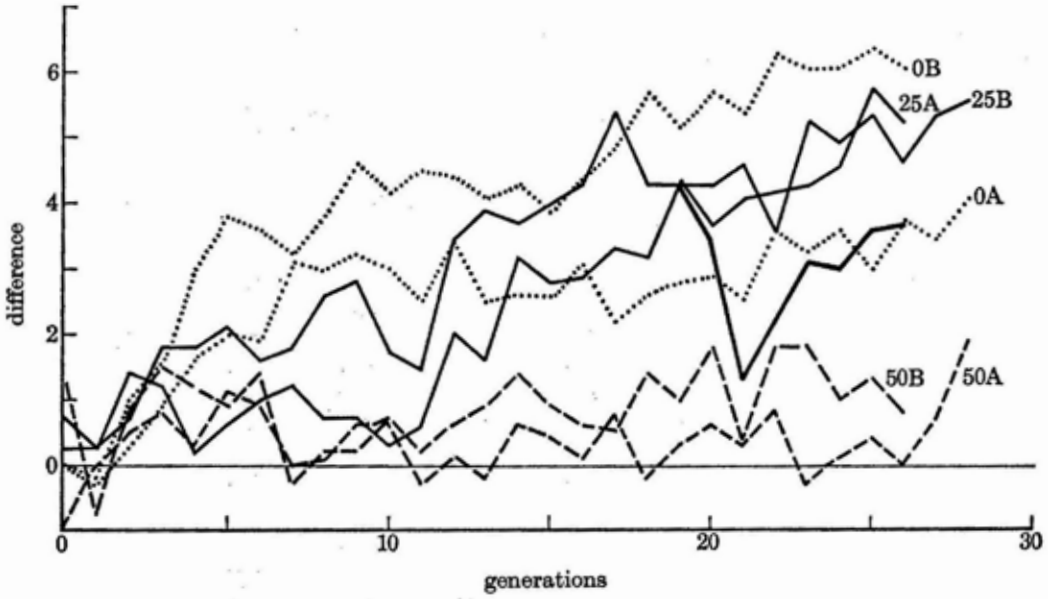

FIGURE 6. Gene flow and divergence under disruptive selection. Each graph represents the difference between the mean chaeta-numbers of the high and low halves of a population. 50A and 50B the two 50 % gene flow lines. 25A and 25B the two 25 % gene flow lines. 0A and 0B the two divergent directional selection pairs of lines. The heavy line is the result of changing the selective migration for 25B (after Millicent & Thoday 1961).

Streams & Pimentel (1961) also using sternopleural chaeta-number in *D. melanogaster* produced consonant results in experiments with asymmetric selection and random migration. They took lines from a base population and selected these, feeding in flies chosen at random from the base population each generation. They showed that with selection of 10 % of the flies assayed 20 % random gene flow allowed considerable divergence, but that 50 % random gene flow allowed slight divergence if any. When they reduced the selection so that they were choosing 40 % of the flies they still obtained some divergence from the unselected control, though it is uncertain that this was in fact a result of selection, for it was their control line rather than the selected lines that changed in mean. Other *Drosophila* experiments have produced generally consonant results.

Pimentel, Smith & Soans (1967) have done a related experiment with house

flies, in which they added the important additional factor, habitat choice, which is of course a factor that may lead to selective migration if the flies exercise the choice open to them. Their experimental system involved communicating boxes. The flies were marked to allow assessment of migration. In one box there were 9 vials of fish food and 1 of banana food and only eggs laid on the banana food were allowed to develop. In another box there were 9 vials of banana food and 1 of fish food, and only eggs laid on the fish food were allowed to develop.

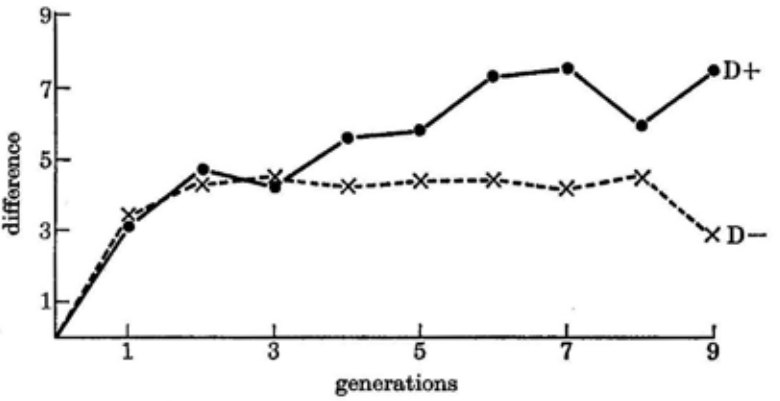

FIGURE 7. Divergence under disruptive selection with 25% gene flow and positively or negatively selective migration.

D^+: Divergence when migrant flies were selected in the same direction as those in the sub-population *to* which they migrated. This selective system is similar to that used for the 25% lines of figure 6, but a different base population (Barton) was used.

D^-: Divergence when migrants were selected in the opposite direction using the same (Barton) population (data from Gibson & Thoday *Heredity* in press).

The result was divergence of two sub-populations, one of which preferred to lay on banana food, the other on fish food, despite some 15% migration between the boxes in the later parts of the experiment. They showed that this divergence was not simply a result of larval conditioning because it was preserved after rearing the flies for two generations on other foods. This elegant experiment not only adds to the evidence that divergence is possible despite migration, but adds to the case that we must take habitat choice and hence selective migration seriously.

II 4. *Isolation*

The question remained whether reproductive isolation itself might result with, or after, this divergence as a result of the same selective forces.

Of the artificial selection experiments that demonstrated that prior isolation is not a prerequisite of divergence those we did first involved forced gene flow and could only result in polymorphism. Two other classes of experiment have been done in circumstances that could permit the development of two isolated populations. One involves random mating, the other, mating choice. With random (or

quasi-random†) mating the gene-flow in any generation depends only on the probability that the 'hybrid' individuals will be included in the selected sample. With mating choice it also depends on the probability that 'hybrid' matings will occur, and on their success relative to the non-hybrid, that is assortative, matings that occur.

Most of these experiments confirm that prior isolation is not necessary if divergence is to occur. Some, however, take us further for they show that isolation may itself arise as Fisher (1930) and Mather (1955) predicted.

(*a*) *Quasi-random mating*

Following a pilot experiment by Thoday & Boam (1961*b*), who were able to maintain a very high variance by disruptive selection with quasi-random mating and full competition between the progeny of all types of mating, Gibson & Thoday (1963, 1964) used a quasi-random mating design without competition to test the efficacy of disruptive selection in these conditions, again using sternopleural chaeta number in *D. melanogaster*. We started these experiments from a newly captured wild stock (Southacre) derived from four fertile wild females caught together in the same dustbin. There were two experiments, each using the same mating system, which is given in table 3 (see also figure 2).

TABLE 3. QUASI-RANDOM MATING SYSTEM

culture	A	B	C	D
	♀ ♂	♀ ♂	♀ ♂	♀ ♂
matings	4H × 4H	4H × 4L	4L × 4H	4L × 4L

The 8 highest and lowest chaeta number flies of each sex are selected from the combined progeny of the four cultures (20 of each sex assayed from each culture in experiment 1 and 8 in experiment 2) and mated as given above.

Selection intensities were lower than those we had used before, for 20 % (instead of 5 %) of the flies assayed were selected in the first experiment and 50 % were selected in the second. The results of the two experiments were essentially the same, though of course 20 % selection was more effective than 50 % selection. Figure 8 illustrates the results with 20 % selection. The divergence of the extreme cultures from the 'hybrid' cultures is striking. Figure 9 illustrates the results obtained with 50 % selection. These experiments leave no doubt of the efficacy of disruptive selection of this kind in increasing genetic as well as phenotypic diversity, and show, once again, that divergence of parts of a population from one another is possible without prior isolation.

The most striking feature of the results, however, was that the hybrid cultures very soon ceased to contribute to the selected flies. In the 20 % selection population, after the sixth generation, all selected high flies came from the H × H culture,

† We define quasi-random mating as mating in the exact proportions expected of random mating.

and all selected low flies came from the L × L culture. The progeny of the H × L and L × H matings were in effect 'sterilized' by the selection for extreme chaeta number. Figure 8 illustrates the overall results of the 20 % selection experiment and shows that in the later generations there was not only no overlap between the HH and LL cultures, but neither overlapped the distributions for the HL or LH cultures. It seems likely therefore that the isolation of the HH and LL sub-lines from one another could have been maintained with even less intense selection than that imposed, which in the latter part of the experiment involved choosing 40 % of the flies from the HH and LL cultures.

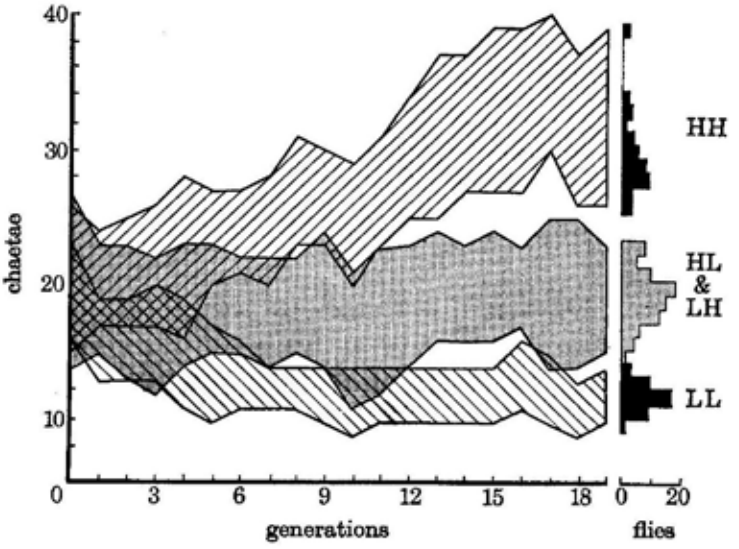

FIGURE 8. Effect of disruptive selection with quasi-random mating – 20 % selection. The figure shows the range of chaeta numbers in each part of the population in each generation, and the distribution curves in the final generation (from Gibson & Thoday 1963).

This conclusion was reinforced by the behaviour of the 50 % selection population. By the sixth generation even in this experiment almost all the selected high chaeta number flies came from the High × High or Low × Low cultures: in fact almost all the flies assayed from these cultures were selected. Likewise the selected low chaeta number flies were almost all from the Low × Low culture and almost all the flies assayed from this culture were selected. The extreme classes of culture had in fact become sufficiently distinct for selection intensity within them to be reduced almost to zero, which was a direct consequence of the design of the experiment. All the artificial selection could do beyond this point would be to eliminate hybrids: it could not cause further divergence of chaeta number, as it could with more intense selection.

These results clearly show that disruptive selection of this type can greatly increase genetic diversity and can induce isolation despite random mating. They further show that even selection intensities as low as those involved in eliminating

50 % of the flies assayed can produce and maintain such diversity and such isolation.

It is evident, however, that there is an important restriction to experiments with disruptive selection under symmetrical quasi-random or random mating. They

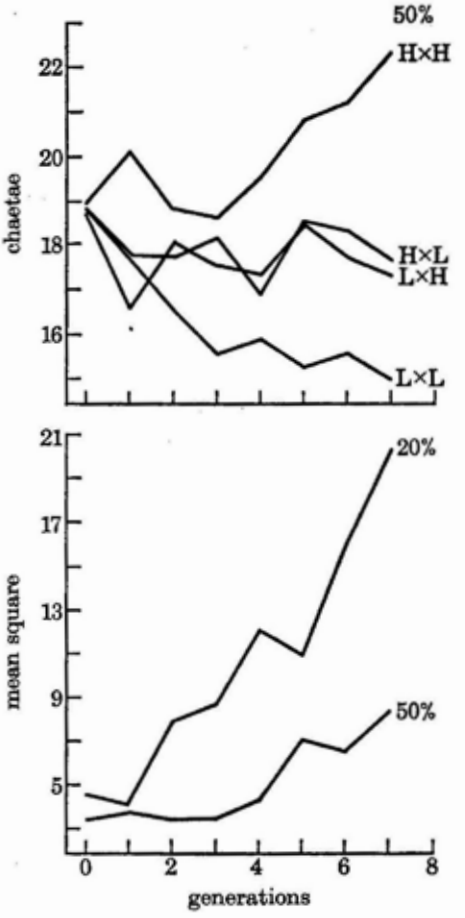

FIGURE 9. Effect of disruptive selection with quasi-random mating – 50 % selection. The upper figure shows the mean chaeta numbers of the four cultures in each generation of the 50 % selection line. The lower figure shows the increase of overall phenotypic variance in this line and, for comparison, in the 20 % selection line (from Gibson & Thoday 1964).

cannot in principle give rise to isolation if selection intensity falls below a minimal value, for below this value selection must necessarily pick out hybrids between the classes selected and hence these two classes are made interdependent when, as Mather (1955) argued, polymorphism not isolation is the expected outcome. If two classes are selected in relative frequency p and $1-p$, the proportion of hybrids in the progeny will be $2p-2p^2$. If selection is symmetrical, 50 % will be hybrids, so that 50 % is the minimum selection intensity that can in principle give rise to isolation.

This restriction does not hold if the classes selected are given mating choice for in these circumstances the number of hybrids before selection may fall below 50%.

(*b*) *Mating choice*

In addition, many experiments have been done to test whether it is possible for disruptive selection with mating choice to reduce the frequency of mating between the phenotypic classes selected. These experiments are of two kinds.

In the first, selection for assortative mating is direct because the material for study is chosen so that hybrids are inviable or sterile or can be unequivocally recognized and thus eliminated by artificial selection. Koopman (1950), Wallace (1954), Knight, Robertson & Waddington (1956), Kessler (1966), Hoenigsberg, Chejne & Hortobagji-German (1966), Dobzhansky & Pavlovsky (1971) and Ehrman (1971) have all shown with various species of *Drosophila* that such selection will promote assortative mating. Paterniani (1969) has published the results of a comparable experiment with maize, in which the frequency of outcrossing between two varieties was reduced from 40% to 4% in 5 generations.

Since Paterniani's experiment seems little known and was most successful, a brief account of it seems desirable here. He started in 1962 with two varieties of maize, one with white flint, the other with yellow sweet kernels. Kernels which result from crosses between these are of course readily recognized as a result of complementary gene action. These two varieties were planted together and, after harvesting and scoring, all ears showing more than 30% hybrid kernels were rejected. Non-hybrid kernels from the remaining ears were planted. In 1963 only ears showing less than 20% hybrid kernels were saved, and this percentage was reduced in 1964 to 5%, in 1965 to 2½%, in 1966 to 0.5% and in 1967 to 0%. This process of selection reduced the frequency of outcrossing from 35.8% to 4.9% in the white flint variety and from 46.7% to 3.4% in the yellow sweet variety. Paterniani was able to show that this great increase of assortative mating was accompanied by development of a difference in flowering time between the varieties. Their mean ear flowering dates were 72.2 and 72.3 days at the beginning of the experiment and 67.0 and 74.5 days at the end. This difference of flowering time was only sufficient to explain the smaller part of the isolation that had developed. By hand pollinating with mixed pollen Paterniani provided some evidence that pollen of the yellow sweet variety competed rather badly with white-flint pollen in the selected white-flint silks. This experiment shows that selection against hybrids can rapidly produce strong isolation between two varieties of maize and complements the results (quoted above) which apply to interspecific and intraspecific differences in *Drosophila*.

The second group of experiments have been run to test whether disruptive selection with mating choice operating on a polygenic character can promote both divergence and isolation together.

Gibson and I (Thoday & Gibson 1962; Thoday 1965) showed that this is possible in two replicate experiments with the same (Southacre) wild stock.

These experiments were run as follows. Four four-pair bottle cultures were set up, and 20 males and females from the progeny of each were scored for sternopleural chaeta-number. The 8 flies with the highest and the 8 with the lowest chaeta-number of each sex were selected from the progeny, which in this and all subsequent generations were of course collected as virgins. The 32 selected flies

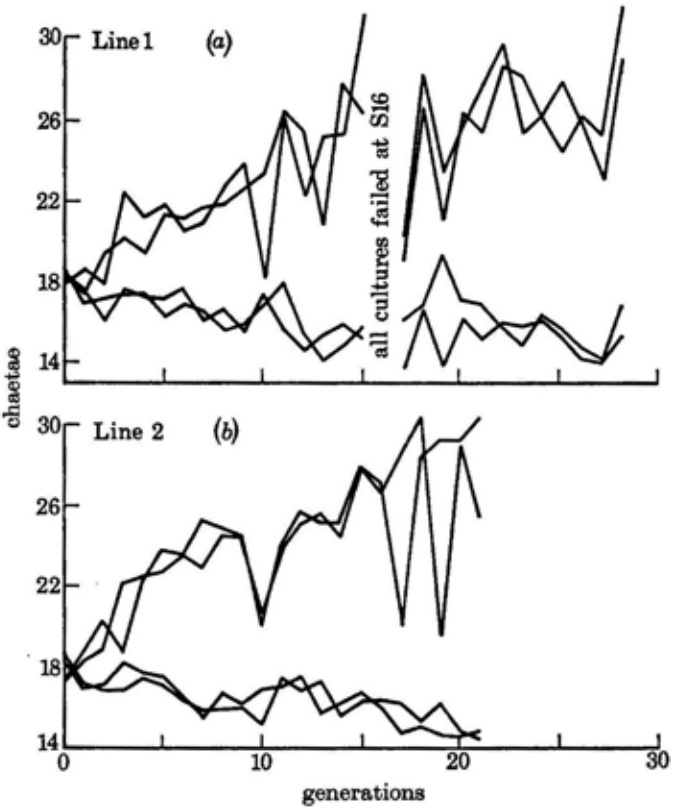

FIGURE 10. Divergence under disruptive selection with mating choice. Each figure shows mean chaeta number in each generation in each of the two cultures with high selected female parents and each of the two cultures with low selected female parents. The upper figure (*a*) refers to the first experiment, the lower (*b*) the replicate experiment. The failure of generation 15 in the first experiment was made good by using residual flies left from the previous generation (data of Thoday & Gibson 1962, and unpublished).

were then placed in the dark† in *the same* 76 mm × 25 mm (3 in × 1 in) vial to mate for 24 hours. They were thus given the choice of mating assortatively, at random, or disassortatively. The males were then destroyed, the females separated again into high and low according to chaeta-number, and the high females were placed four each into two bottles to lay, the low females likewise.

This process was repeated in each generation, the flies always being selected

† Light was not controlled in the first experiment until generation 14.

without regard to the culture from which they came, though records of their culture of origin were of course kept.

The first experiment gave rapid divergence (figure 10) between the progeny of high and of low females and by the 12th generation the two distribution curves had a clear gap between them (figure 11). Tests made by forcing hybridization showed that the hybrids had intermediate chaeta-numbers and that the existence of the gap must be due to lack of hybrids in the line.

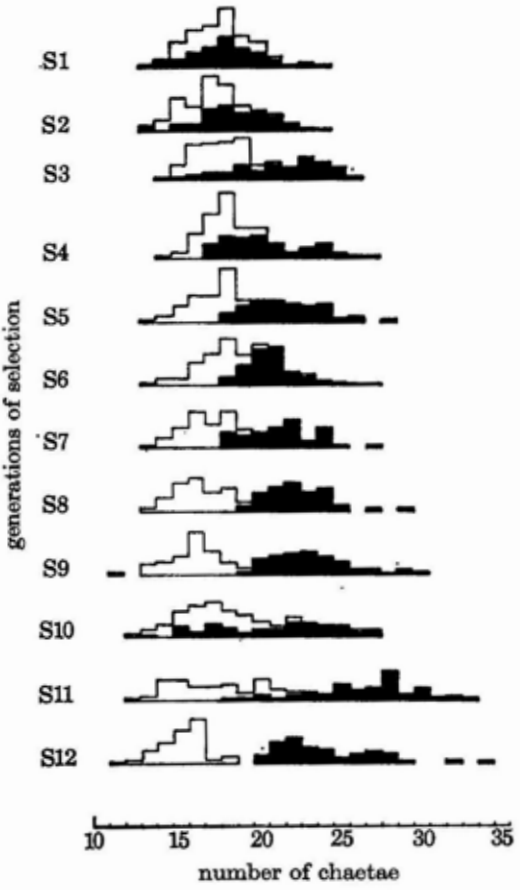

FIGURE 11. Distributions of chaeta number under disruptive selection with mating choice: first Southacre experiment. In each distribution the white area represents the progeny of low females and the black area that of high females. In the first generation they are alike; by generation 12 there was no overlap (from Thoday & Gibson 1962).

The second experiment worked even more rapidly than the first, the two distribution curves separating in generation 7 (figure 10). Thereafter they remained separate, except in occasional generations, when the difference between halves was reduced. This, as has been discussed by Thoday & Gibson (1970*a*) and Robertson

(1970), is a necessary consequence of the small number of parents used in such experiments, which leads to large variance of the mean mating frequencies, together no doubt with inviability, etc., arising from inbreeding.

Two types of test were made on this line with some regularity. In each generation forced matings were made to give information concerning the chaeta-numbers of the progeny of hybrid and non-hybrid matings. These showed that a few hybrids occurred on the low side of the line, but in most of the later generations there were none on the high side. Figure 12 shows the state of this population at generation 21, and that of the original population at generation 28.

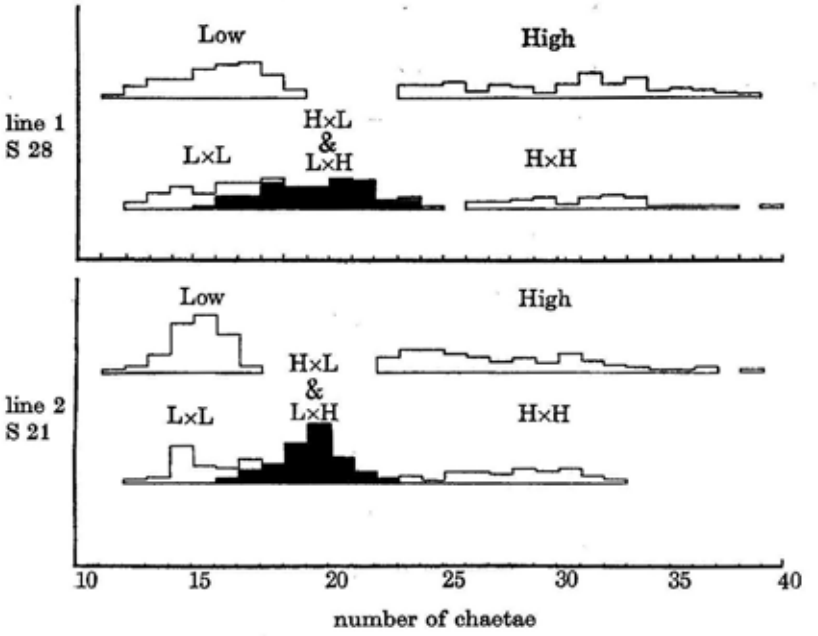

FIGURE 12. Distribution of chaeta number in the two experimental populations derived from the Southacre stock. The upper half of each figure shows the discontinuous distribution of chaeta numbers in the experimental population. The lower half shows the distributions produced by forced quasi-random mating. The black area represents the combined progenies of H × L and L × H matings. It can be seen that few hybrid flies occurred in experimental populations themselves (after Thoday 1965).

The other tests were mating 'choice' tests, which were done as follows. Extra flies were reared, scored, selected and mated as if to maintain the line. But after mating, the 16 females were placed in 16 cultures so that their individual progenies could be assayed for chaeta-number. The mean chaeta numbers of hybrid and non-hybrid cultures were sufficiently distinct to permit recognition of the progenies of the different types of mating unequivocally. The accumulated data are given in table 4. Hybrid progenies occurred at less than half the expected frequency and there were few sterile cultures, suggesting that preferential mating was involved.

Comparable mating tests were done on the isolated stocks kept from the original experiment and results from these are also given in the table.

These tests seemed clearly to show that a substantial part of the reproductive isolation in these lines was the result of differential mating success.

TABLE 4. RESULTS OF 'MATING CHOICE' TESTS ON THE ISOLATION LINES

(*a*) Combined results of 8 tests on line 1

H♀ × H♂	H♀ × L♂	L♀ × H♂	L♀ × L♂	failures
42	5	6	36	39

(*b*) Tests of line 2

generation tested	H♀ × H♂	H♀ × L♂	L♀ × H♂	L♀ × L♂	failures
7	12	3	3	12	1
8	14	2	6	10	–
9	10	4	6	7	5
10	8	4	3	13	4
19	27	2	8	20	7
(4 tests combined)					
total	71	15	27	62	17

Similar experiments have been tried since in a number of other laboratories and one in our own, without producing isolation (Scharloo 1964; Crenshaw 1966; Robertson 1966; Scharloo *et al.* 1967*a*, *b*; Chabora 1968; Barker & Cummins 1969; Robertson 1970; Thoday & Gibson 1970*a*). Thoday & Gibson (1970*a*) (see also Scharloo 1971; and Thoday & Gibson 1971) have discussed in detail why we think this negative evidence provides little information concerning the frequency with which wild populations may have the capacity to respond in this way. Detailed argument led to the conclusion that only two suitable stocks of *Drosophila* had been tested. Of these one, Southacre, produced isolation, the other, from Buenos Aires, did not, though divergence was substantial and the population became polymorphic. We may now add a third stock, for Beardmore and Al Baldawi are repeating this experiment using exactly the conditions that Gibson and I used and using a newly captured wild stock, a matter that we considered of great importance. Professor Beardmore has kindly permitted me to describe the results to date. They started with the progeny of four females newly captured in the same vinegar factory in Greece. The results are very similar to ours. Response of sternopleural chaeta number was rapid (figure 13), the distribution curves have separated, and they have shown that hybrids have intermediate chaeta numbers (figure 14). This further experiment strengthens the view that the possibility that divergence and isolation may be produced together by disruptive selection must be taken seriously.

Murty & Sharma (personal communication) have also obtained relevant results using *Brassica campestris* var. Brown Sarson, an oil seed crop. Their paper (1972) is not yet published, and the descriptions of the mating system in the disruptive lines that are available are a little difficult to interpret, but the details seem to be as follows. They selected for early and late flowering time, which is of course

a potential isolating character of itself. They used disruptive selection on several base stocks, and there were comparable divergent directional selection lines for comparison. In the disruptive selection lines the early and late plants were allowed

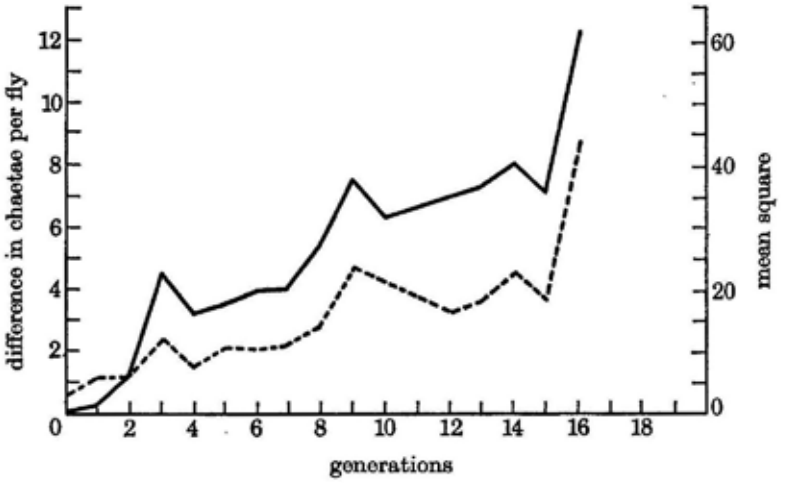

FIGURE 13. Results of Beardmore and Baldawi's mating choice experiment on their Greek population. The solid line shows the difference for each generation between the mean chaeta number of the progenies of high and low females. The broken line shows the phenotypic variance of the population (by kind permission of Professor Beardmore).

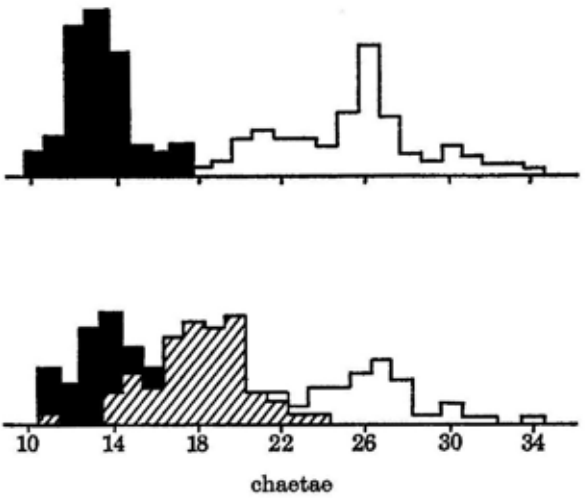

FIGURE 14. Distribution of chaeta number in Beardmore and Baldawi's experimental population and in their quasi-random mating tests: Generation 16. Upper distribution for the population: progenies of low females in black, of high females in white. Lower distribution for the quasi-random mating test: L × L black, H × L and L × H hatched, H × H white. The results are very similar to those given in figure 12 (by kind permission of Professor Beardmore).

to open pollinate, but early × late and late × early progenies were also produced by controlled pollination. From 400 plants of the combined progenies, the 10 earliest and the 10 latest (i.e. 5%) were selected for 6 generations. Divergence in the disruptive lines was rapid and they became isolated to an extent that made crossing the early and late parts of the population impossible. A striking feature of these experiments was that divergence was more rapid and the final difference in flowering time was 25% greater under disruptive than it was under divergent directional selection. This is presumably because the gene flow permitted in the disruptive selection lines in the earlier part of the experiment allowed transfer of appropriate genes from one half of the population to the other. Another interesting feature is that some of the early flowering products of the disruptive selection experiments have proved to give high yield over a wide range of agro-climatic conditions. As a result a new variety has been released showing that disruptive selection has applied value, probably because of the greater opportunity for recombination implicit in disruptive selection programmes.

IV. Relevance of the results to natural populations

The results outlined above differ from the theoretical expectations put forward by Mather (1955) only inasmuch as they have shown effects of greater magnitude and have produced them more quickly than could have been anticipated. In some respects, however, their applicability to natural populations is controversial. Much of the controversy depends on our judgement concerning the degree to which and the intensity with which we suppose disruptive selection to be operating in nature.

(*a*) *Disruptive selection and genetic diversity*

The heterogeneity of habitats seems, in fact, often to be underestimated by ecological geneticists. But Levins (1968, p. 87) lists a number of examples of heterogeneity; surface soil pH on a calcareous hillside may vary with depth of soil from 4.1 to 6.5 over very short distances; and the use of the phrase 'rough herbage' to describe the environment of a population of say *Cepea* is becoming a botanical joke. Most natural populations live in heterogeneous habitats and some selection for diversity must be quite general. I therefore have little doubt that disruptive selection plays some significant part in the origin and maintenance of the genetic heterogeneity that has been shown to be so widespread. The relative uniformity of habitat of some apomicts, and the tendency of plants to change to more close inbreeding when agricultural man actually selects for uniformity and makes the environment more uniform by controlling such factors as soil condition and the number and variety of competitors, adds cogence to this view.

In considering the causes and functions of the genetic diversity generally found in natural populations, disruptive selection therefore needs to be taken into account. As an illustration of the way our thinking should go in this direction we need only consider a little of the evidence concerning just one environmental factor which

seems relevant to *Drosophila*. The environmental factor is yeast. The findings are as follows:

1. Baits with different yeasts are differentially attractive to *Drosophila* (Dobzhansky & da Cunha 1955).

2. Different populations of the same species show different yeast preferences (Dobzhansky & da Cunha 1955).

3. Species prefer the yeasts that best support their development (Cooper 1960). I am not aware whether this finding has been shown to apply to differing genotypes within a species.

4. The relative viabilities of homozygotes for different chromosomes from the same population change with change of yeast (Dobzhansky, Pavlovsky, Spassky & Spassky 1955).

5. In cage populations the relative fitnesses of different inversion genotypes change with change of yeast (da Cunha 1951).

6. Cage populations provided with a variety of yeasts and media maintain a higher degree of heterozygosity for electrophoretic enzyme variants than do cages providing a more uniform environment in these respects, as has been shown in the natural disruptive selection experiment of Powell briefly described on p. 114.

These results together seem to me to show that unless the concepts of heterogeneous selective forces and of habitat choice are considered, discussion concerning genetic load, and concerning the neutrality of alleles in natural populations, can only be of interest to those who need models that satisfy the aesthetic sense of the mathematically minded. To apply their conclusions to nature can only bring confusion. Disruptive selection, and other forms of frequency dependent (see Huang, Singh & Kojima 1971) and density dependent selection, must be ubiquitous in nature, and must be responsible for some part of the ubiquitous genetic diversity we find. It is our job to find out how large that part is, not to polarize each other into the extreme positions of naive pan-selectionist or even naiver neutralist.

(*b*) *Overt polymorphisms*

In recent years the distinction between the general genetic diversity and segregational polymorphism has become blurred, as biochemical techniques for the classification of genotypes have confirmed that overt polymorphisms, as we may call classical polymorphisms, are especially obvious examples of a general phenomenon. Overt polymorphisms may however be much more complex as became clear from the discussions of Fisher (1930).

It was such polymorphisms that Mather (1955) had in mind in his classic discussion of disruptive selection.

The more complex polymorphisms produced by disruptive selection for polygenic characters in the laboratory are not doubt simpler than those found in nature. But all the essential features of the 'natural' systems are there in the negative assortative mating polymorphism of Thoday (1960), see figure 4. It is one of the attractions of work on natural polymorphic populations, especially that of Clarke

& Sheppard (for review see Ford 1964), that these workers have been able to reveal much of the genetic architecture of the systems involved. It is one of the aspects of disruptive selection experiments that pleases this author most, that he and his associates have not only been able to produce polymorphic populations in the laboratory, using a classic polygenic character, but also to analyse these populations and find out so much about the specific genes involved. The development of techniques for the location of specific polygenes in these and other investigations of effects of selection (see Thoday 1961, 1967*a*,*b*,*c*) and the demonstration that some of the relevant loci can be handled with sufficient precision in breeding experiments, bid fair to add substantially to our understanding of selection and of the genetics of continuous variables generally. That the genetic system thus revealed in our analysis of this polymorphism should be so like those of natural polymorphisms adds great strength to the view put forward by Mather (1955) and also supported by Clarke & Sheppard (1960, 1962) that they have similar causes in disruptive selection.

This view is not I think controversial, so that we may turn to a different kind of polymorphism found in nature. Giesel (1970) has published an account of some natural populations of the limpet *Acmaea digitalis*, in which disruptive selection appears to be maintaining what we must regard as a primitive polymorphism. Discontinuity among these limpets is imposed in each generation on an initially continuous distribution exactly as has occurred in the earlier stages of most disruptive selection experiments. The young limpets vary in shell colour but show no clear bimodality. The variation seems to be largely genetic. As the limpets develop some of them move from the dark rock on to white barnacles, those with lighter shells moving to barnacles in greater frequency. By the time the limpets are 10 mm in diameter the frequency of the intermediate shell colours has been reduced so that the adults show a clear-cut bimodality with light shelled individuals on barnacles, and dark shelled individuals on the rocks. In situations that are less exposed to predators when the tide is out the polymorphism among adults is less pronounced.

The maintenance of this polymorphism clearly involves heavy selection pressures and a high cost in terms of selective deaths. However the reproductive capacity of the limpets is evidently adequate to carry this cost, and it is already less than it might be because of the habitat choice. We may expect that this polymorphism will evolve in time in other ways, and develop more economical polymorphisms as some of the experimental populations have done.

(*c*) *Disruptive selection and divergence*

The demonstrations that disruptive selection, with or without selective migration and habitat choice, can promote divergence despite migration are relevant to our understanding of clines and of the possibility of adaptive divergence of populations in habitats that are marginal to the ecological tolerance of a species, whether these habitats are well within or at the edge of the species' geographic distribution. Most relevant experiments have involved rather intense selection (but see Gibson &

Thoday's (1964) experiment p. 123), so that it would be desirable if more experiments at lower selection intensities and with less gene migration were done. Nevertheless we know that in some natural situations, selection intensities as high as or higher than those used in our experiments may occur.

Barber & Jackson (1957) published an example showing that very intense selection indeed operates in altitudinal clines of *Eucalyptus*. From 570 m to 690 m (1900 ft to 2300 ft), in the area they studied, the adult trees are uniformly 'green', but seedlings from open pollinated green trees produce some glaucous progeny down to 570 m. 'Glaucous' forms increase in frequency with increasing altitude reaching 100% at 910 m and above, but some seedlings from open pollinated glaucous trees produced green progeny up to 990 m, indicating that selection at the tails of the cline is absolute.

Bradshaw and his colleagues in their work on various plants, especially *Agrostis*, have provided comparable evidence that disruptive selection may promote evolution of adapted populations in environments marginal to the normal ecological tolerance of the main populations of a species, despite intense gene flow from those main populations (see especially Antonovics & Bradshaw 1970). Snaydon (1970) has shown that comparable results may be produced in mosaic environments, by demonstrating micro clines in *Anthoxanthum* across the boundaries between the Rothamsted plots that have been fertilized differently for many decades. Doggett & Majisu (1968) show the same to be true for wild and cultivated *Sorghum*, and Doggett (1965) has suggested the same for maize. Such studies show clearly enough that intense disruptive selection is effective in nature. Even though they may be extreme examples some of them involve more or less cryptic environmental variables and suggest that ecological geneticists should be very wary of assuming uniformity of apparently uniform environments.

(*d*) *Isolation*

The most controversial question is whether the demonstrations that disruptive selection can lead to strong isolation are relevant in nature. So controversial has this been that this aspect of disruptive selection has in my view been overstressed, as Thoday (1967*d*) and Thoday & Gibson (1970*a*) have pointed out. Disruptive selection would have to be considered an important topic even if it had not been shown that isolation could result. Its importance does not stand or fall on the question of isolation.

Nevertheless, our experiments (Thoday & Boam 1959; Millicent & Thoday 1960, 1961; and, most especially, Thoday & Gibson 1962) raised old questions anew because they disposed of what had hitherto been regarded by some as a cogent theoretical objection to the concept that divergence and isolation might evolve sympatrically.

The possible modes of primary speciation can be divided into three classes (see Mayr 1959 for a discussion of the history of these ideas).

The first is purely allopatric. Divergence and isolation develop in populations

separated by a geographic barrier. In this process divergence is a consequence of geographic isolation, and reproductive isolation is a consequence of differences due to founder effect, drift and the divergent directional selection such geographic isolation implies.

In the other two modes of speciation, reproductive isolation results from selection against hybridization itself. In the first of these, divergence occurs allopatrically, but reproductive isolation results because the two populations meet again, when selection operates to reduce the reproductive wastage consequent upon low fitness of the progeny of hybrid matings. In the second, both divergence and isolation occur more or less sympatrically through disruptive selection.

I believe that these three classes of speciation process are less distinct than their protagonists think. The distinction between them depends much on the meaning given to the word allopatric. This, however, is a word we can define precisely, and whose meaning we can relate to the meaning of the term disruptive selection. Allopatric populations are populations that are geographically isolated from one another to such a degree that there is not sufficient gene migration between them to promote their genetic convergence. Since in theory (see, e.g., Falconer 1960) random migration amounting to 1 individual per generation is enough to prevent two populations diverging by drift alone, whatever their size, divergence above this very low level of migration must require disruptive selection as we define it.

Strictly allopatric speciation is therefore a rigidly definable and restricted concept. Any other kind of primary speciation involves some element of sympatry and some element of disruptive selection.

A comparable definition of strictly sympatric speciation is difficult, and perhaps not profitable, to devise, except in relation to models and experimental populations. In the relevant experiments the individuals of the two selected classes were strictly sympatric while mating, though not while the eggs developed into adults. Any hybrids were however sympatric with one or other non-hybrid class. The conditions of these experiments are therefore very closely analogous to those in which Thorpe (1930, 1939) envisaged host races might diverge (see also Bush 1969), if we assume that, in these, males reared on different host plants initially mate at random with the females that lay eggs preferentially on those differing hosts. Mayr (1942) at one time thought that such random mating would prevent divergence. Our experiments show that this is not so. But in the real situation, it is difficult to believe that mating would in fact ever be random, for the micro-geographic separation of the host plants would itself be expected to lead to some assortative mating. Divergence might therefore need lower selection pressure than those used in our experiments.

It is likewise with most situations we can imagine except where the different classes selected are interdependent. Whether the environment be mosaic or clinal, there will be micro-geographic distances separating the parts of the population that are differentially selected, and, since most dispersal is over short distances, this will result in some assortative mating, which habitat choice may often accentuate.

(The rare type effect (Petit & Ehrman 1969) may sometimes act in the contrary direction.)

The issue therefore is not whether strictly sympatric speciation occurs. It is whether populations that are geographically partially isolated do in fact ever split into completely isolated populations as a result of disruptive selection, or whether complete prior geographical isolation is an essential prerequisite of speciation in the biological (as distinct from the taxonomic) sense.

Considering the matter in this context it is clear that disruptive selection is involved in speciation. Every hybrid zone which is not expanding (see Remington 1968), and every case where hybrids are formed in nature but are inviable or sterile, provides an example where disruptive selection is maintaining species differences. Every example of introgressive hybridization that involves a man-made hybrid habitat (Anderson 1949; and see the excellent example of *Fucus*, Burrows & Lodge 1951) is a testament that hybrids between the species are being formed but eliminated by selection before we can see them. Examples can be found in the reviews of Mayr (1963), Stebbins (1950), Grant (1971) and Heslop-Harrison (1964). More direct evidence is also available that species pairs exist which have overlapping distributions and hybridize readily, but where the hybrids do not establish themselves often enough to have been found in nature. (See, e.g., Nobs (1963) on *Ceanothus*.)

We may however go further than this, for there is evidence that isolation does in fact develop in some disruptively selected natural populations. McNeilly & Antonovics (1968) and Antonovics (1968) have shown that a measure of isolation has developed in some lead mine populations of *Anthoxanthum* and of *Agrostis tenuis*. *Phlox pilosa* normally has pink flowers, but where it occurs together with populations of *Phlox glabberina*, which is also pink, it is white-flowered. Levin & Kerster (1967) and Levin & Schaal (1970) have shown that the differential flower colour leads to assortative mating. Clarke & Murray (1969) are of the view that the occurrence of sinistral snails at high frequency in areas where one species, elsewhere dextral, overlaps the distribution of another dextral species have the same explanation as the white-flowered *Phlox*.

Evidence is also accumulating that isolation is stronger between sympatric than between allopatric pairs of populations of species with overlapping ranges (Dobzhansky & Koller 1938; Ehrman 1965; Mettler & Nagle 1966 (Drosophila): Stephens 1946; Kruckeberg 1957; Grun & Radlow 1961; Grant 1965, 1966, 1971 (various plants): Rubinoff & Rubinoff 1971 (fish)).

Combining these lines of evidence, we are forced to the view that some species differences are maintained by disruptive selection, that disruptive selection is actively involved in the maintenance of differences between local populations, and that in some of these it is resulting in the production of a measure of isolation, or has been involved in the enhancement of isolation that may have originated allopatrically. We cannot therefore maintain the view that pure allopatric speciation is the only mode of speciation that occurs. Among others, Stebbins (1964),

Grant (1966), Spieth (1968) and White (1968) expressed similar views, and Crosby (1970) has published the results of relevant simulation experiments.

It remains to discuss some of the factors that need to be taken into account in considering whether a disruptive selection situation is likely to promote isolation rather than polymorphism, either of which may be regarded as possible adaptations to the environmental heterogeneity that imposes the disruptive selection itself, even if the selected classes are free to be independent if they can.

Given environmental variation within the range of gametic or zygotic dispersal, two related factors seem likely to be of major importance. The first is the nature of the available genetic variance, for this determines the relative ease with which dominance or isolation may evolve. Clearly the evolution of a dominant supergene will render the heterozygotes as fit as one of the parental classes and will therefore prevent selection working against hybridization, whereas the evolution of isolation will reduce the frequency of hybrids and therefore prevent selection working in favour of dominance. In a clinal situation, however, as Fisher (1930) argued, dominance may evolve in different directions at the different ends of the cline, which may therefore break in the middle if isolation variance is available.

The second factor is the adaptedness of the hybrids themselves, for unless they are maladapted, there is no reason for isolation or dominance to evolve. Adaptedness of the hybrids will of course depend on the existence of special environments such as intermediate conditions at the boundaries of the environments imposing the disruptive selection or in the middle of clines. Two considerations suggest however that the hybridization is likely to have disadvantages where the two disruptively selected components of a population overlap in gametic or zygotic distribution.

First, even if a single locus, two-allele response to disruptive selection be envisaged, in a situation where three environments are available such that each genotype has one niche that favours it, a one-locus system would be an inefficient response. This follows from the fact that an efficient response requires adjustment of three genotype frequencies to niche size, whereas a one-locus two-allele system with random mating has only one way of manipulating genotype frequency, that is by manipulating gene frequency, and the zygotic frequencies of the three genotypes cannot therefore be adjusted independently. In consequence unless the sizes of the three niches happen to be such as to support approximately Hardy–Weinberg frequencies, a more complex genetic system with 3 alleles and dominance, or two loci with dominance and epistasis, would be necessary to fill them.

Second it is unlikely that adaptation will be a single locus phenomenon, so that recombination in hybrids will give products unfit in all environments (Wallace & Vetukhiv 1955) unless tightly linked dominant supergenes evolve.

Our judgement concerning the likelihood that isolation will evolve under disruptive selection when the different optima selected can be independent therefore depends in part upon our judgement whether it is easier for isolation to evolve than dominant supergenes. There is plenty of evidence that both may happen, but we

shall need a good deal more knowledge before we can judge their relative probabilities which will differ according to the genetic systems of the populations.

Mayr (1963) who has of course been the major proponent of pure allopatric speciation, though he does also admit (p. 554) some of the possibilities discussed here, has argued (p. 472) that our experimental results in this respect are not likely to be relevant in nature. He says: 'The severity and absoluteness of the selection, the complete prevention of gene flow, and the elimination of mutual competition are, of course, a set of artificial conditions that could scarcely be expected ever to occur in nature.'

Some of these criticisms are less cogent than others. 'The severity of the selection' is less than in some known natural situations (see p. 134). It is difficult to know what Mayr means by 'absoluteness of selection' but if he means that it was truncation selection, this might be relevant. But 'the complete prevention of gene flow' is *not* a condition of the experiments. In so far as it was complete it was a consequence of the disruptive selection and is in fact the point at issue. 'The elimination of mutual competition' is a valid restriction but any habitat choice would limit it. Another restriction that Mayr does not mention, is the maintenance of equal numbers of the two classes selected. These *may* be conditions severely limiting the relevance of these experiments to nature, but this is a matter of judgement.

And it is judgement that must be made with caution. The key objection to our artificial selection experiments must clearly be that high selection intensities are used and that we judge that natural selection intensities will usually be lower than this. But it must be remembered that the design of the experiments which have given rise to reproductive isolation is also as extreme as it could be in another respect; the circumstances of mating were pure sympatry. Judgement concerning the relevance of such experimental results to natural conditions must therefore depend on judgement whether and to what extent relaxation of this condition of total sympatry may permit the same results to be produced, albeit more slowly, with selection intensities that we judge it reasonable to postulate in nature.

It must be remembered that our definitions of population vary with our purposes. At one end we may define a population as a purely sympatric group of individuals interbreeding at random, but this is an ideal concept only appropriate to model builders and designers of laboratory experiments. At the other end we may define a population as including all the members of a species or even a set of species between which there is any gene exchange. Many real populations will fit neither of these extreme definitions and there will be sets of sub-populations between which there is less than random gene exchange, which can diverge from one another as a result of differential selection pressures, sometimes aided by habitat choice and by selective migration. The evidence that isolation between such parapatric, quasi-sympatric, or quasi-allopatric populations can be enhanced by selection seems to be good. Purely allopatric speciation is unlikely to be the only mode by which the origin of two species from one has occurred in evolution.

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