

POPULATION INTER-RELATIONSHIPS

I. EVOLUTION IN MIXTURES OF *DROSOPHILA* MUTANTS

A. P. C. SEATON and J. ANTONOVICS

Department of Agricultural Botany, University College of North Wales, Bangor

Received 2.iv.66

1. INTRODUCTION

SOME of the most important influences that come to bear on an organism stem from its relationships with other organisms. This is particularly true of plants which grow associated in dense communities. Nevertheless, the evolutionary changes in the relationship between forms resulting from such associations have been little studied.

Wright and Dobzhansky (1946) have shown that different chromosome arrangements have different adaptive values in crowded population cages, and Dobzhansky (1950) and others record changes in such values under these conditions. Buzatti-Traverso (1955) showed that a population from which two mutant genes had been eliminated could subsequently eliminate these mutants more quickly if they were re-introduced into the population. Similarly, Moore (1952) found that the relative numbers of *Drosophila simulans* and *melanogaster* emerging from mixtures could be altered in favour of *simulans* by previous experience of mixing. Pimentel (1964) and Pimentel *et al.* (1965) showed that the blowfly becomes better able to survive in the presence of the housefly after it has suffered drastically in mixtures of the two.

Many other workers have shown that the ability to persist or gain ascendancy in mixtures is inherited; for example, Mather and Cooke (1962) and Gale (1964) have shown this in *Drosophila*, Sakai and Gotch (1955) in barley, and Lerner and Ho (1961) in *Tribolium*.

The present experiments examine the changes which may occur in populations as a result of interaction in mixed cultures. Experiments of the type originated by de Wit (1960) have been used to examine critically the interactions between components in a mixture. These experiments differentiate clearly the nature of the evolutionary changes in the relationships between two species that can occur when these species are grown together.

The words "competition" and "competitive ability" have caused considerable confusion. Most workers have failed to examine the nature of relationships between species before coming to agreement, and have attached phenomena to these words without allowing that they are currently used in a wide variety of contexts. The use of these terms has been fully discussed by Birch (1957), Harper (1961), and Donald (1963). Since this paper shows how these words may be inappropriate and misleading when used in their normally understood manner, their use has been avoided.

2. MATERIALS AND METHODS

Wild type and dumpy (wing) mutant flies of *Drosophila melanogaster* were used throughout. The dumpy in both experiments and the Dronfield wild type in the second experiment were obtained from the Genetics Department, Cambridge. The wild type in the first experiment was a well established stock of unknown origin. None of the stocks were highly inbred. All the experiments were performed in half-pint milk bottles using a maize/treacle medium seeded with dried yeast granules and all kept at 23°C. in a dark incubator.

In the selection stages of the experiment progeny from an equal number of wild type and dumpy fertilised females were collected as virgins. Flies of each type were then allowed to mate amongst themselves to produce fertilised females which were then used to repeat the cycle. It was shown (Section 5) that there was natural selection for flies which were superior under these conditions. In all the selection stages the dumpy were introduced two days earlier than wild type, since with simultaneous introduction the number of dumpy was drastically reduced. All parents were removed four days after their introduction.

In the testing stages of the experiment

- (i) fertilised females of wild type from the selection regime were put with an equal number of fertilised females of stock dumpy,
- (ii) fertilised females of dumpy from the selection regime were put with an equal number of fertilised females of stock wild type.

Here, the two types were introduced simultaneously and the parents removed after four days. The number of each type emerging after eight days from emergence was counted at each generation. The selection and testing scheme summarised in fig. 1. Two experiments were performed, the second to confirm the first and to analyse the situation in more detail.

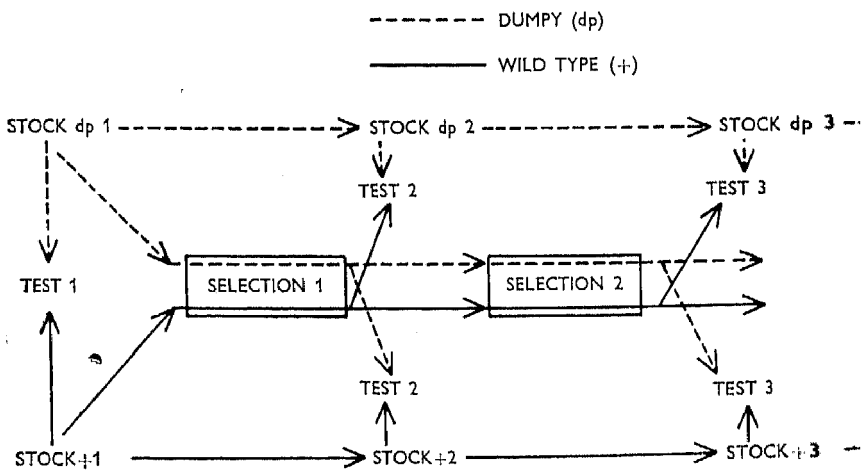


FIG. 1.—Diagrammatic scheme of selection and testing procedure.

3. THE FIRST EXPERIMENT

Three replicates were used throughout, but separate replicate lines were not maintained. There were twenty flies per bottle and selection was for three generations.

(a) *Changes in inter-relationship*

The proportion of dumpy emerging from the selection regimes increased from 48 per cent. to 59 per cent., suggesting that either dumpy or wild type were changing. At each generation the flies were tested as already outlined. The tests showed (fig. 2) that the proportion of dumpy emerging increased in selected dumpy/stock wild type, but decreased in selected wild type/stock dumpy. Therefore both dumpy and wild type emerging from mixed cultures showed improved reaction to their associates.

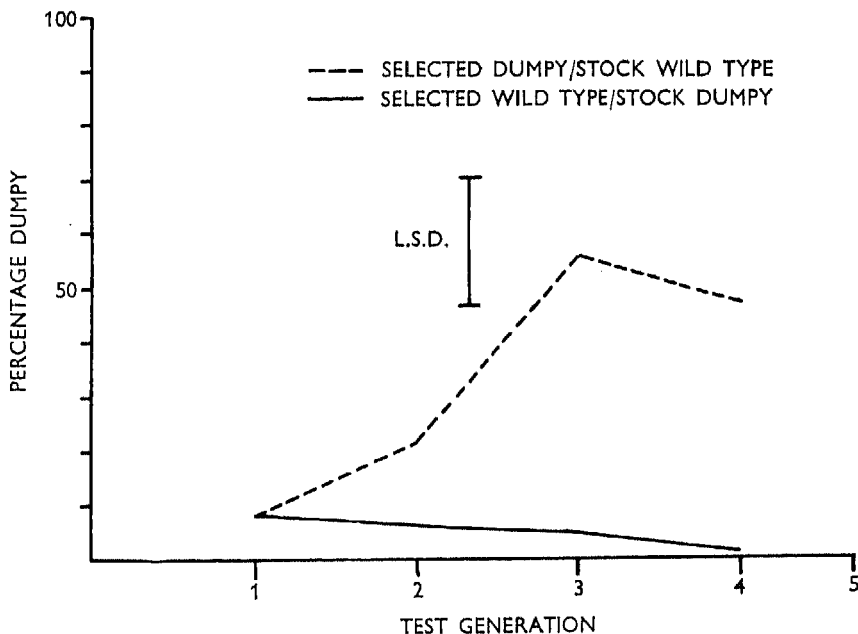


FIG. 2.—Change in frequency of dumpy emerging from tests. First experiment.

(b) *Components of change*

To study the changes that occurred in the flies as a result of selection, two attributes were measured:—

- (i) *Activity.* Flies were put singly in stoppered tubes. Each tube was jolted until the fly was at the bottom and the stopper removed. The time taken for the fly to escape was recorded in seconds. The escape time (table 1) decreased in both the selected types, significantly so in dumpy. In selected dumpy the variance of escape time also decreased; all signs of “very slow flies” were lost.
- (ii) *Wing length.* Variance in wing length (table 2) went down in the selected types, significantly so in wild type. The average wing length decreased in wild type but increased in dumpy:

both changes are highly significant. This is rather unexpected and can have several explanations (see discussion).

TABLE 1
Means and variances of escape times

	Wild type		Dumpy	
	Stock	Selected	Stock	Selected
Mean escape time in seconds	18.7	17.5	33.3†	25.4†
Variance	21.9	33.1	274.3*	81.5*
Coefficient of variation	25.0	32.9	49.7	35.5

* Difference significant at 5 per cent. level.

† Difference significant at 1 per cent. level.

TABLE 2
Means and variances of wing length

	Wild type		Dumpy	
	Stock	Selected	Stock	Selected
Mean wing length in mm.	4.70*	3.61*	4.03†	4.40†
Variance	0.161‡	0.39‡	0.050	0.034
Coefficient of variation	0.854	1.730	0.555	0.412

* Difference significant at 0.1 per cent. level.

† Difference significant at 0.1 per cent. level.

‡ Difference significant at 1.0 per cent. level.

4. THE SECOND EXPERIMENT

Four replicate lines were used throughout but there was no replication within the lines for the tests nor for the de Wit experiments. There were 12 flies per bottle and selection was for three generations.

(a) *Changes in inter-relationship*

The frequency of dumpy emerging from the selection regimes increased from 38 per cent. to 63 per cent. In the tests (fig. 3) the proportion of dumpy emerging showed a progressive increase in selected dumpy/stock wild type. Dumpy also increased in the tests of selected wild type/stock dumpy, but more slowly.

This seemed somewhat unexpected. However, a test between the final stocks of dumpy and wild type showed that they had changed; therefore relative to the stocks the frequency of dumpy decreased in selected wild type/stock dumpy tests.

The considerable changes in the behaviour of the stocks is probably because they had been obtained just before the experiment and were new to the medium.

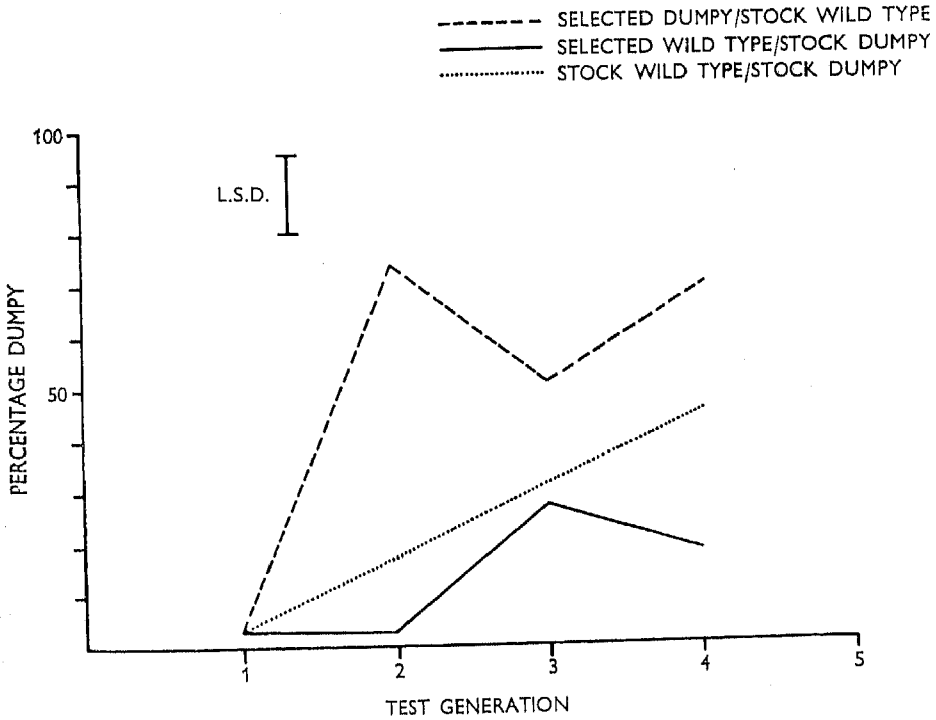


FIG. 3.—Change in frequency of dumpy emerging from tests. Second experiment.

(b) Components of change

At the end of this experiment, egg-laying capacity was measured by the number of eggs laid after 24 hours on food contained in a vial enclosed in a stoppered tube. The egg-laying capacity (table 3) of

TABLE 3
Egg laying means and variances

	Wild type		Dumpy	
	Stock	Selected	Stock	Selected
Number of eggs/fly	23.8*	36.8*	8.3	13.6
Variation	47.4	132.2	84.4	49.2
Coefficient of variation	28.9	31.3	110.7	51.6

* Difference significant at 1.0 per cent. level.

the selected flies was considerably greater than that of the unselected stocks.

5. THE NATURE OF THE CHANGES IN POPULATION INTER-RELATIONSHIPS

The interaction of dumpy and wild type was examined by comparing the performance of the types in pure culture with their performance in mixtures. The proportions of the two in mixture were varied while total numbers were kept constant. The experiments were performed in a similar way to the tests, and all started with 12 fertilised females.

The results have been plotted in two ways (de Wit, 1960). Firstly, separate yields of the types in the mixtures, total yields of the mixtures, and yields of pure cultures have been plotted on the same graph: these are known as Replacement Series Graphs. They show the contributions of the two types to the total yield. Secondly, the log of the ratio of the two types put into the mixture has been plotted against the log of the ratio coming out. Such Ratio Diagrams can predict the changes in the relative frequency of the two types over future generations, providing their genetic constitution and the experimental conditions were to remain the same. Vertical lines on the graphs represent limits beyond which ratios are too high or too low to be attained by the experimental design. To predict the behaviour of more extreme ratios we would have to use more flies, and thus change density.

Least significant differences are not indicated on the Replacement Series Graphs, since

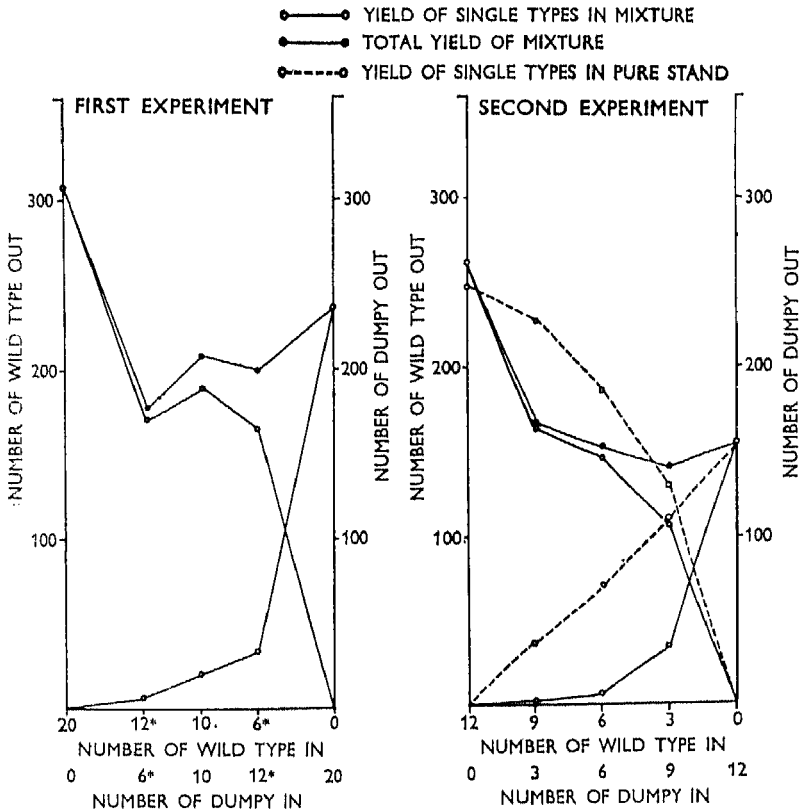
- (i) the variance of populations of the two components in the mixture are not independent,
- (ii) each pair of points would require its own L.S.D.; variance differed with proportion, and
- (iii) the variance in the second experiment is likely to be inflated as replicate lines were used and although there were differences between lines, the overall pattern of the Replacement Series Graphs showed remarkable consistency.

The following are a good guide to the error met with in the experiment. Overall L.S.D. ($P < 0.05$) for number of flies for experiments on initial stocks of the first and second experiment = 61.8; for experiments after four generations = 32.5; for experiments after one generation of relaxed selection = 56.9.

(a) Performance of the initial populations

The situation at the start of both experiments is shown in fig. 4. Wild type contributes proportionately more to the overall yield than dumpy. If they had contributed proportionately equal numbers, the lines for yield of each type in mixture would be straight. The overall yield of the mixture is less than that of either pure stand. The mixture does not utilise the environment as well as the pure cultures. In the second experiment comparison of the yields of each type in mixture

with the yields of that type by itself confirms there is reduction of each type by the other. The degree of reduction of dumpy is far greater than that of wild type. Over all densities, the number of dumpy emerging is reduced by 60.5 per cent., while wild type is reduced by only 21.4 per cent. This reduction is a measure of the selection pressures acting.



*Note: total number of flies only 18

FIG. 4.—Replacement series graphs showing inter-relationship of wild type and dumpy at the start of experiments one and two.

The Ratio Diagrams (fig. 5) show that whatever ratio of dumpy flies was put into the mixture, a lower ratio of dumpy emerged. Since the slopes of the lines are significantly different ($P < 0.05$) from unity, the lines cross the line of unit slope and at a high frequency of dumpy, dumpy and not wild type would be at an advantage. However, the point of intersection is only reached at, or beyond, the experimental limits. The possible advantage of dumpy is therefore only theoretical. But the graphs do show that the relationship between stock dumpy and stock wild type is frequency dependent.

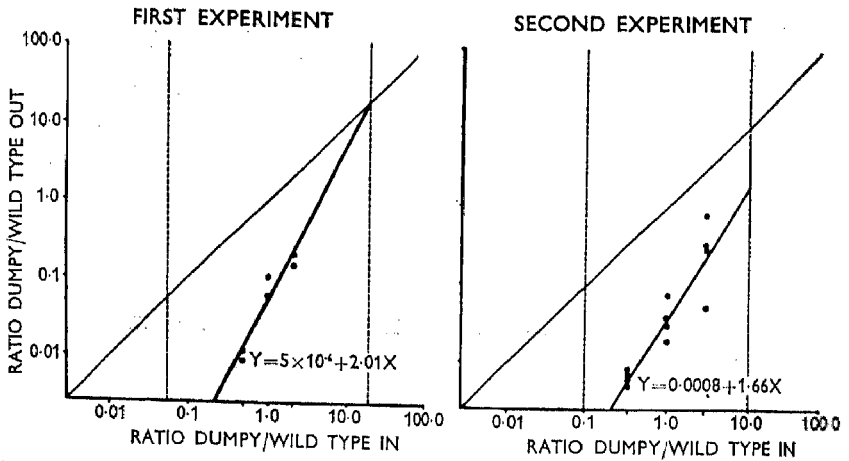


Fig. 5.—Ratio diagrams showing inter-relationship of wild type and dumpy at the start of experiments one and two (derived from data shown in fig. 4).

(b) *Performance of populations after three generations of selection*

The flies from the second experiment were used to assess the performance of the types after selection. The results are shown as Replacement Series Graphs in fig. 6 and as a Ratio Diagram in fig. 7.

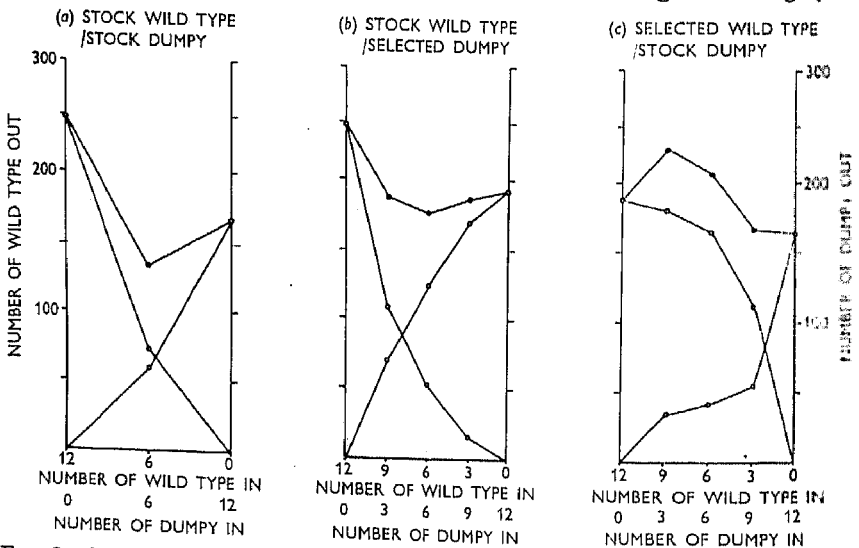


Fig. 6.—Replacement series graphs showing the effect of selection on the inter-relationships of wild type and dumpy.

(i) *Stock wild type/stock dumpy* (figs. 6a and 7a). The performance of the types in stock generation four has changed compared with the original material (figs. 4a and 5a). Wild type as well as dumpy is now depressed in mixtures. The Ratio Diagram shows that the input and output ratios now do not differ greatly: the slope of the line is not significantly greater than unity. However, the outer points of this line had to be obtained by extrapolation from the Replacement Series

Graph, so conclusions can only be tentative. The overall pattern is nevertheless similar to that shown by the initial stocks.

- (a) STOCK DUMPY/STOCK WILD TYPE (b) SELECTED DUMPY/STOCK WILD TYPE (—→)
(c) STOCK DUMPY/SELECTED WILD TYPE (—→)

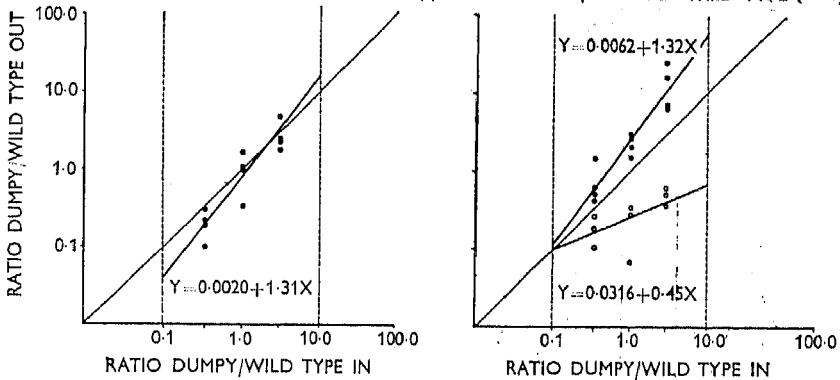


FIG. 7.—Ratio diagrams showing the effect of selection on the inter-relationships of wild type and dumpy (derived from data shown in fig. 6).

(ii) *Stock wild type/selected dumpy* (figs. 6b and 7b). The relationship between the two types has been changed by selection and dumpy now outyields wild type. The depression of total yield is slightly less than that in mixtures of unselected stocks: the increase in the yield of dumpy has been only partly at the expense of wild type.

Selected dumpy in pure culture yields more than the original stock. Selection has not only increased its yield in mixtures but has also improved its reaction to itself in pure cultures.

The Ratio Diagram bears out these changes: dumpy now increases its proportion in the next generation. The relationship is not frequency dependent (slope of line not significantly different from unity), and if this condition persisted dumpy would eventually eliminate wild type.

(iii) *Selected wild type/stock dumpy* (figs. 6c and 7c). Selected wild type shows improved reaction to dumpy. As with selected dumpy, the improved performance of selected wild type has been gained without a proportionate reduction of dumpy. Also the mixture yields much more than either pure culture. This shows that the two types exploit the environment better than before selection. Selection has apparently caused dumpy to avoid wild type, not “hit it harder”: it has improved ecological combining ability (Harper, 1961).

The Ratio Diagram shows these effects more clearly. The line has a slope significantly less than unity ($P < 0.05$). This implies that the mixture is self-stabilising (de Wit, 1960): if there is initially a high proportion of dumpy, dumpy is at an advantage. The population therefore, theoretically at least, tends towards an equilibrium given by the interception of the ratio line with the line of unit slope.

(iv) *Selected wild type/selected dumpy*. The relation between these types was examined only after a generation of relaxed selection (see below).

(c) Performance of populations after relaxation of selection

After selection, selected and stock cultures were kept as pure stands for one generation and the relationship between the lines examined. This time only mixtures with equal proportions of wild type and dummy (6 : 6) were used. The general pattern (fig. 8 and table 4) is slightly

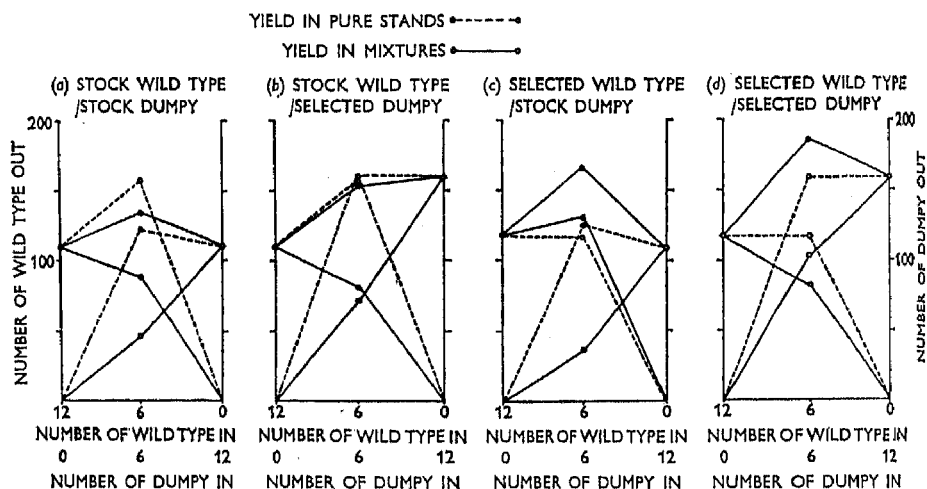


FIG. 8.—Replacement series graphs showing inter-relationships after a generation with relaxed selection.

TABLE 4

Numbers and ratios of dp : + emerging from 6 : 6 mixture

	Mean numbers		Mean ratio (Log scale)
	dp	+	dp : +
Stock + / Stock dp.	46.3	88.5	0.52 : 1
Stock + / Selected dp.	73.8	83.3	0.89 : 1
Selected + / Stock dp.	37.3	131.0	0.29 : 1
Selected + / Selected dp.*	104.0	82.5	1.11 : 1

* Based on two replicates only.

different from that obtained immediately after selection. Now all mixtures yield more than pure cultures. This cannot be easily explained, but the experiment was performed by a different worker and slightly different amounts of food may have been used. The detailed pattern is, however, the same. Selected dummy yields more than stock dummy in mixtures with stock wild type, and selected wild type yields very much more than stock wild type in mixtures with stock dummy. The overall yield of the mixtures of selected and stock types was markedly greater than the yield of the pure cultures at density of 12

flies, particularly in selected wild type/stock dumpy. The increase in yield of the selected types in mixture is again not accompanied by a corresponding decrease in the yield of the stock types.

To estimate the selection pressures acting on the types, their yields in mixtures were compared with their yields as pure types at half density (table 5). The selection pressures in the mixtures involving

TABLE 5
Reduction in number emerging (selection pressure)
due to presence of the other type in mixture

Mixture	Type	Percentage reduction	Total percentage reduction
Stock + / Stock dp.	+ dp	36.0 44.0	40.0
Stock + / Selected dp.	+ dp	32.8 35.9	34.4
Selected + / Stock dp.	+ dp	-17.7 45.4	27.7
Selected + / Selected dp.	+ dp	20.3 20.6	20.5

Differences between mixtures significant at 5.0 per cent. level.
Differences between types significant at 1.0 per cent. level.
Mixture \times type interaction significant at 5.0 per cent. level.

selected types have in every case been reduced compared with those in the stock wild type/stock dumpy mixture, particularly in selected wild type/selected dumpy. It is remarkable too, that when either selected dumpy or selected wild type is mixed with the opposite stock type, the selection pressure on this stock is *the same* as in stock/stock mixtures, whereas that on the selected type is *decreased*. This confirms that selection has not resulted in an increased power of one component to suppress the other, but in an increased ability to avoid it.

6. DISCUSSION

There is abundant evidence that direct selection can cause changes in *Drosophila*. Nevertheless, selection for performance in mixtures has been rarely studied and only infrequently observed. Lerner and Ho (1961) and Gale (1964) failed to detect such changes, but used inbred lines, and even Moore (1952) who concluded "competitive ability can be developed by selection . . . in comparatively short periods of time", found this in one line out of twenty and then only in *Drosophila simulans* and not *melanogaster*. Although there is insufficient work to decide

whether the success of a population in mixture is in general a character that can readily be selected, the present experiments suggest that it can be easily changed.

The speed with which the changes occurred is surprising, but it is perhaps less remarkable since the selection pressures acting on the mixtures were quite high. Rapid changes have also been found by Pimentel *et al.* (1965). The experiments described here tend to invalidate both long-term predictions (whether from experimental or theoretical models) as to the outcome of growing two types together as well as tests of population fitness involving elimination of one type by another. For example, Barker (1965) considers that genetic changes in mixed populations may complicate the estimation of fitness, but does not stress this point.

Lerner and Ho (1961) suggest that failure to select for superior performance in mixtures may be because the characters concerned are determined by non-additive effects, but the work of Sakai and Gotoh (1955) and Mather and Cooke (1962), who find an additive effect for performances in mixtures on chromosome III of *Drosophila*, argues against this. The latter do, however, detect fairly large interactions between chromosomes. In this respect, the work on evolution of heterosis in population cages by Dobzhansky (1950) is interesting.

Since the performance of individuals in a mixed population may depend on many attributes it seems not unlikely that it could be altered by selection. For example, larger wings in dumpy, shorter wings in wild type, greater egg-laying capacity and greater activity were all detected in the selected populations. Selection for larger wings in dumpy would be expected, since the mutation tends to reduce wing size and smaller wings in wild types may imply smaller flies; Buzatti Traverso (1955) also found decreased wing length in selected populations. Migratory activity of *Drosophila* has been shown to be an important factor in the persistence of types in mixtures by Sakai (1965). More generally, Bakker (1961) has shown a complex of factors affecting performance of *Drosophila* in mixtures.

The success of one species in a mixture (usually termed "competitive ability") is generally attributed either to the ability of that species to produce a greater proportion of offspring in the next generation at the expense of the other or to its ability to reduce the numbers of the other species without itself changing. This work shows that both these ideas are too simple. The success of one component may depend on its ability to avoid the other without necessarily having any effect on it. Such a relationship makes the use of the terms "competitive ability" and "competition", with all their specific connotations extremely confusing. There is the added complication that the relationships described may be frequency dependent.

De Wit's (1961) method of presenting such data as Replacement Series and Ratio Diagrams is an elegant procedure for defining the nature of changes in population inter-relationships, and if the yields

different densities of pure cultures are included, even more information can be gained since changes in selection pressure from the other species can then be assessed. The experiments described here, while by no means an exhaustive application of these methods, show their power in analysing inter-relationships of populations.

Evolutionary changes in mixed populations have been discussed by Pimentel (1964, 1965). He suggests that if two species, A and B, make demands on a limiting environmental resource and one, say A, becomes dominant, then A will become subject mainly to intraspecific selection, whereas B will be subject to interspecific selection. He argues that selection will then lead to the improvement of B with respect to A so that B may become the more abundant species. A will then be under primarily interspecific and B intraspecific selection. Oscillating populations of A and B then develop, eventually leading to a state of relative stability. Pimentel gives evidence for such fluctuations in frequencies of house flies and blowflies in experimental populations.

The results presented here do not entirely conform to the situation described by Pimentel. Firstly, improved performance of dumpy towards wild type went hand in hand with improved performance in reaction to its own density. Secondly, the inter-relationship that evolves is one where the mixture has immediate self-stabilising properties, whereas Pimentel envisages an oscillating system. Here, stability is the product of evolution towards the occupation of separate niches by the two strains and a reduction of selection pressure. There is much evidence that closely related genotypes (Khan, 1963) or even sexes (Putwain, 1966) do have slightly different ecological requirements and are thereby able to form stable associations (Gause, 1934). Williamson (1957), Ludwig (1959) and Slobodkin (1963), as well as de Wit (1960), have produced theoretical models describing this kind of situation. While rapid cycles of selection by alternating inter- and intra-specific stress may occur, the divergence of requirements (the occupation of alternative niches) seems a far likelier outcome of selection in mixed populations.

Darwin envisaged in *The Origin of Species* that evolution may entail development of stable associations due to increased diversity—

“the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many widely diversified places in the polity of nature, and so be enabled to increase in numbers.”

The experiments described here show how “nature red in tooth and claw” can lead to peaceful coexistence.

7. SUMMARY

1. The performance of populations of dumpy and wild type *Drosophila melanogaster* in mixtures (where interbreeding was prevented) was

shown to be a character that could be rapidly changed by natural selection.

2. The change was studied by Replacement Series Graphs and Ratio Diagrams. An increase in the proportion of one type emerging from a mixture was due more to its ability to avoid interference than to its ability to suppress the other.

3. It is misleading to describe these changes in terms of changes in "competitive ability".

4. Such changes in inter-relationship can lead to the evolution of stable associations between different populations.

Acknowledgments.—We are indebted to Mr D. Machin for help with the statistics. We also wish to thank Professor J. L. Harper and Dr. A. D. Bradshaw for their help and encouragement and Mr. P. D. Putwain for critically reading the manuscript.

8. REFERENCES

- BAKKER, K. 1961. An analysis of factors which determine success in competition for food among larvae of *Drosophila melanogaster*. *Archs. neerl. Zool.*, 14, 200-281.
- BARKER, J. S. F. 1965. The estimation of relative fitness of *Drosophila* populations. IV. Experiments of *D. pseudoobscura*. *Genetics*, 51, 747-759.
- BIRCH, L. C. 1957. The meanings of competition. *Am. Nat.*, 91, 5-18.
- BUZATTI-TRAVERSO, A. A. 1955. Evolutionary changes in components of fitness and other polygenic traits in *Drosophila melanogaster*. *Heredity*, 9, 153-186.
- DE WIT, C. T. 1960. On competition. *Versl. Landbouwk. Onderz. Ned.*, 66, 8.
- DOBZHANSKY, T. 1950. Genetics of natural populations. XIX. Origin of heterosis through natural selection in populations of *Drosophila pseudoobscura*. *Genetics*, 35, 288-302.
- DONALD, C. M. 1963. Competition among crop and pasture plants. *Adv. Agron.*, 15, 1-118.
- GALE, J. S. 1964. Competition between three lines of *Drosophila melanogaster*. *Heredity*, 19, 681-699.
- GAUSE, G. F. 1934. *The struggle for existence*. Baltimore, Williams & Wilkins, 163 pp.
- HARPER, J. L. 1961. Approaches to the study of plant competition. *Symp. Soc. exp. Biol.*, 15, 1-39.
- KHAN, M. A. 1963. *Physiologic and genetic analysis of varietal differences within Linum usitatissimum (Flax and Linseed)*. Ph.D. Thesis, University of Wales.
- LENER, I. M., AND HO, F. K. 1961. Genotype and competitive ability in *Tribolium* species. *Am. Nat.*, 95, 329-343.
- LUDWIG, W. 1959. Die Selektionstheorie. In Herberer, G., *Die Evolutionen der Organismen*. Stuttgart, Fischer, 662-712.
- MATHER, K., AND COOKE, P. 1962. Differences in competitive ability between genotypes of *Drosophila*. *Heredity*, 17, 381-407.
- MOORE, J. A. 1952. Competition between *Drosophila melanogaster* and *Drosophila simulans*. II. The improvement of competitive ability through selection. *Proc. Nat. Acad. Sci., Wash.*, 38, 813-817.
- PIMENTEL, D. 1964. Population ecology and the genetic feed-back mechanism. In *Genetics Today. Proceedings of the XI International Congress of Genetics, The Hague, Netherlands, September 1963*. Pergamon Press, 483-488.
- PIMENTEL, D., FEINBURG, E. H., WOOD, P. W., AND HAYES, J. T. 1965. Selection, spatial distribution, and the coexistence of competing fly species. *Am. Nat.*, 99, 97-109.

- PUTWAIN, P. D. 1966. The mechanism governing sex balance in *Rumex acetosella* L. In preparation.
- SAKAI, K. 1965. Contributions to the problem of species colonisation from the viewpoint of competition and migration. In Baker, H. G., and Stebbins, G. L., *The Genetics of Colonising Species*, Academic Press, 215-239.
- SAKAI, K., AND GOTOH, K. 1955. Studies on competition in plants. IV. Competitive ability of F_1 hybrids in barley. *J. Hered.*, 46, 139-143.
- SLOBODKIN, L. B. 1963. *Growth and regulation of animal populations*. Holt, Rinehart, & Winston. 184 pp.
- WILLIAMSON, M. H. 1957. An elementary theory of interspecific competition. *Nature, Lond.*, 180, 422-425.
- WRIGHT, S., AND DOBZHANSKY, T. 1946. Genetics of natural populations. XII. Experimental reproduction of some of the changes caused by natural selection in certain populations of *Drosophila pseudoobscura*. *Genetics*, 31, 125-156.

MENDEL

DARWIN

MORGAN

HEREDITY

Edited by

Kenneth Lewis
Oxford

501
14-3
V. 22
1967
copy 2

Kenneth Mather CBE FRS
Southampton

John Thoday FRS
Cambridge

Cyril Darlington FRS
Oxford

John Jinks
Birmingham

David Catcheside FRS
Canberra

An International Journal of Genetics founded
in 1947 by C D Darlington and R A Fisher in
collaboration with G W Beadle, T Caspersson,
Th Dobzhansky, B Ephrussi and Ø Winge

Oliver and Boyd
London and Edinburgh

BOVERI

BATESON

WILSON

JOHANNSEN

GALTON

WEISMANN

VILMORIN

VAVILOV

LINNAEUS

DE VRIES

SPALLANZANI