

# COURTSHIP PROCESSING IN *DROSOPHILA MELANOGASTER*.

## I. SELECTION FOR RECEPTIVITY TO WINGLESS MALES

By ROBERT M. COOK\*

(1973)

Department of Psychology, University of Sheffield, England

**Abstract:** The first experiment was a selection procedure designed to increase the receptivity of *Drosophila melanogaster* females to males whose courtship had become less effective through attenuation of wing vibration. The clearest response was in the percentage of females receptive per generation, but changes were also detected in courtship duration and latency to courtship. The two selected and two control lines were hybridized in experiment 2, and the hybrid of the selected lines (Selx) was found to maintain the adaptation to selection of its parents. The relative receptivity of all female types was compared in experiment 3. The results demonstrated that adaptations had occurred in the females' courtship processing, rather than merely in the males' ability to court.

The last decade of research with *Drosophila* courtship behaviour has seen a considerable advance in the understanding of the manner in which the female is stimulated by the courtship emitted by the male. The observation by Sturtevant (1915) of the importance of the male's wings in the courtship display has been confirmed by experiments locating the receptors involved in the perception of wing vibration by the female (Petit 1958; Manning 1967b; Burnet, Connolly & Dennis 1971), and by experiments involving the augmentation of the courtship of wingless males through simulation of components of the wing vibration display (Bennet-Clark & Ewing 1967, 1969).

It has also been suggested that the female processes the courtship she receives. Manning (1967a) refers to a 'courtship summation system' in the female which 'summates' the courtship received from the male through various sensory channels. The rapidity with which the female summates courtship is reflected by the time taken from the start of courtship to the point at which copulation occurs; this time is referred to as the 'courtship duration'. Since there is little independent evidence that females of *Drosophila melanogaster* do use information from diverse sensory modalities in responding to courtship, I prefer to refer to such a system in the female as the courtship 'processing' system. Evidence that such a system exists is presented by Cook (1973).

### Experiment 1

The temporal course of a courtship is directly dependent upon the presence and nature of the wing vibration display. Nevertheless, it is apparent that when the wings are removed from the males a certain proportion of females will still be inseminated, although after a longer courtship duration. Ewing (1964) studied the relationship between wing area of the male and receptivity of the female, and found it to be linear. Thus the phenomena of wingless courtship may repay further study, since the stimulation of the female is not so abnormal as completely to inhibit receptivity but is sufficient so to alter radically its time relationships. Artificial selection for receptivity to wingless males should produce adaptations which give insight into the processes controlling the female's acceptance under these and normal conditions of courtship.

A situation similar to this was studied by Crossley (1963), who selected against hybridization between lines of *D. melanogaster* carrying *vestigial* and *ebony* markers. The *vestigial* mutant lacks functional wings and it is largely because of this that its courtship is impaired. Thus Crossley was selecting for the *vestigial* female to accept wingless males in preference to *ebony* males, and for the *vestigial* males to court the *vestigial* females, and similarly for *ebony*. Both the courtship emission of the males, and the discrimination of the females, measured by their rejection responses (see also Connolly & Cook 1973), were changed.

In this experiment a simplified paradigm was employed which did not involve the use of

\*Present address: Laboratoire de Génétique Expérimentale des Populations, Université des Sciences et Techniques du Languedoc, F34-Montpellier, France.

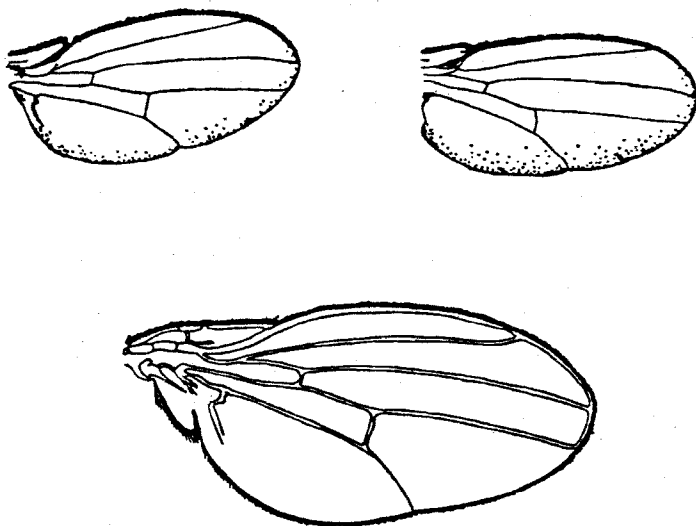


Fig. 1. Comparison of amputated (above) and normal (below) wings.

mutants and where the emphasis was on acceptance by a female of normal males with amputated wings.

#### Design

The selection paradigm involved selection on both sexes, rather than just on the female. It would have been possible to make all tests on selected females with males drawn randomly from a different population, but, since the selection schedule completely determined the mating scheme, any advantages of selecting on one sex alone could be outweighed by the effects of dilution of the selected gene pool by the extraneous genes from the males' population. The males used were therefore from the same lines as the females, and there was opportunity for adaptation to occur in either or both sexes, although the major interest was focussed on the female.

Unlike Manning's (1961) experiment, selection took place in a single pair context which provides a greater opportunity to exert the selection pressures more precisely. One can, for example, measure latency to courtship as well as courtship duration, and base the selection on only one of these parameters. Single pair mating may have the effect of slowing down gains from selection, since no choice of mates is available.

The method of wing amputation was simple. A pair of fine cutting forceps was used to snip off the wings of the etherized males. The extent

of this operation is similar to that of Ewing's (1964) operation A. More exact measurements of the degree of amputation and its variability have been made from the amputated wings remaining after the operation. The mean area of the amputated wings, in arbitrary units, was  $50.96 \pm 1.186$  (5 per cent confidence limits). Thus the variation was very small in comparison with the absolute area. Figure 1 shows the approximate range of wing amputation, compared with a normal wing.

Bastock (1956) found no reduction in the persistence in courtship of males after they had undergone wing amputation. This was borne out by a preliminary study in which the behaviour of winged and wingless males was compared.

Duplicate independent selected lines were kept, as recommended for example by DeFries (1967), in order to be able to assess with greater reliability the veracity of any response to selection, and the meaningfulness of correlated changes. In this experiment two lines from the same base population were selected independently, called VBL 1 and VBL 2, VBL signifying the attempt to make them 'vibrationless'. Control lines were also maintained, again in duplicate. These are referred to as VBL 1 control and VBL 2 control.

#### Animals

The base population used was Canton strain *D. melanogaster* which had recently been re-

ceived from Dr W. Kaplan's laboratory in America. There was one main reason for using this strain. As noted in the introduction, reduction in wing area leads to an increase in courtship time. Selection for reduction of this courtship time could work on overall receptivity, or upon specific mechanisms controlling courtship processing, the latter being more desirable for the present experiment. It was therefore advantageous to take a strain with high initial receptivity so that the chances of getting a response merely by increasing overall receptivity would be reduced. The Canton strain fulfilled this criterion.

The experimental populations were reared in half-pint milk bottles, and on the standard yeasted agar/oatmeal/molasses medium of the laboratory. Oviposition was allowed to occur in the culture bottles by the parental animals for 2 to 3 days. Culture temperature was  $25^{\circ} \pm 1^{\circ}\text{C}$ .

### Selection Paradigm

The experiment was designed to select unidirectionally for acceptance of wingless males, and to decrease the acceptance time in so doing.

The population to be selected was collected and sexed on the morning of eclosion. The females were kept in food vials in densities of twenty-five per vial, whilst male density ranged up to thirty per vial.

Measures were made on days two and three after eclosion (counting the day of eclosion as day nought), both in the morning and afternoon. Courtship occurred readily at all these times. The wings of the males were amputated between 20.00 and 22.00 hours on the day before measurement.

For each of the selected lines sixty pairs were observed in small moulded plastic mating cells, measuring 18 mm diameter by 6 mm deep and fitted with sliding Perspex lids, and two bungs. For each pair the time of onset of courtship and copulation was recorded, so that latency to courtship and courtship duration could be calculated. Courtship duration is here defined as the absolute time between onset of courtship and occurrence of copulation, with no correction for breaks in courtship.

Any pairs which had not shown courtship in 30 min were separated, and the female paired with a new male, timing being started again.

Observations for each pair were continued for 2 hr. The fastest ten pairs to mate were then removed from the cells and set in a fresh culture bottle to produce the next generation.

Males and females from the control lines were measured in a similar way. The control lines were not measured at every generation of selection, and the median sample size was forty-nine pairs. All the control animals were discarded after their receptivity had been measured, and the next generation was obtained from ten pairs selected at random from the culture bottles.

Generations of selection will be referred to in the form  $S_j$ .

**Results of selection: The first thirty generations.**

### Percentage Receptivity

Fluctuations between generation means due to environmental factors in selection experiments have been considered by Sokal & Hunter (1956). One means of reducing such variability between generations on graphical records involves the use of the moving average rather than the raw data.

The percentage receptivity (the percentage of females receptive in any sample, for this experiment) has been processed as a moving average on a three generation basis. This is plotted in Fig. 2. It includes the first thirty generations of selection, and shows both the selected and control lines.

Selection was relaxed at  $S_{12}$  and  $S_{14}$  due to the presence of a mould in culture.

The controls vary below 50 per cent receptivity for the duration of the selection. Both selected lines however, tending to be below 50 per cent for the first fifteen generations, consistently exceed this level in the latter half of the experiment.

The results of a trend analysis on these data are shown in Table I. Only the linear, and other components which were of significance, are shown. The only significant non-linear component is for VBL 2 control, which had a cubic component. A small correlation between the control lines was also found, but was not significant. Such a correlation could reflect macro-environment effects common to the cultures.

### Courtship Duration

The distribution of times of those females accepting the wingless males is extremely positively skewed, having a long tail of acceptances over the duration of the observation period. A three-generation moving average for median courtship duration is plotted in Fig. 3. It is difficult to distinguish a trend which is due to selection. The main outstanding feature is that

Table I. Experiment 1. Trend Analysis on Raw Proportional Receptivity

	<i>F</i> linear	<i>df</i>	<i>P</i>	Linear correlation	Regression coefficient
VBL 1	20.07	1, 27	<0.001	0.653	1.23
VBL 2	11.25	1, 28	<0.01	0.535	1.16
VBL 1 Control	1.95	1, 16	NS	0.329	0.72
	3, 74 cubic	1, 16	NS		
VBL 2 Control	0.05	1, 16	NS	0.055	0.12
	8.46 cubic	1, 16	<0.025		

Correlation between controls = 0.292; *df* = 15; NS.

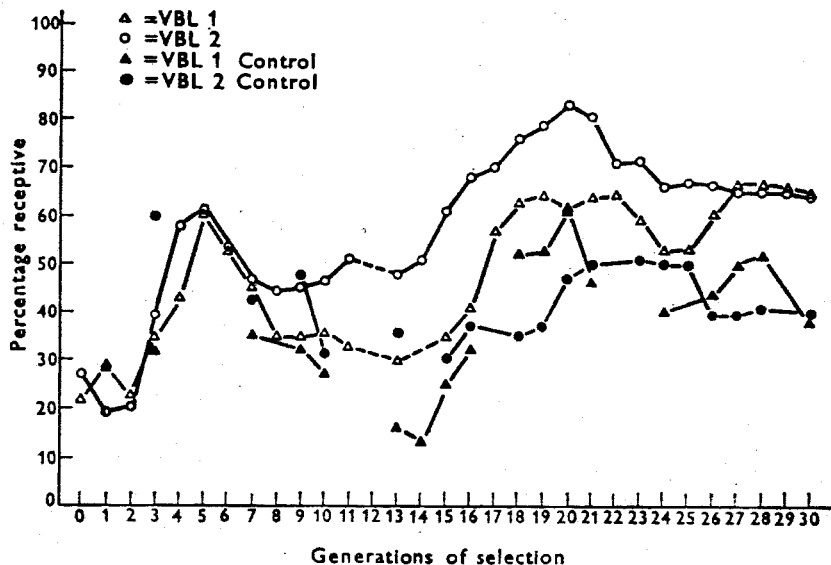


Fig. 2. Three generation moving average for percentage receptivity.

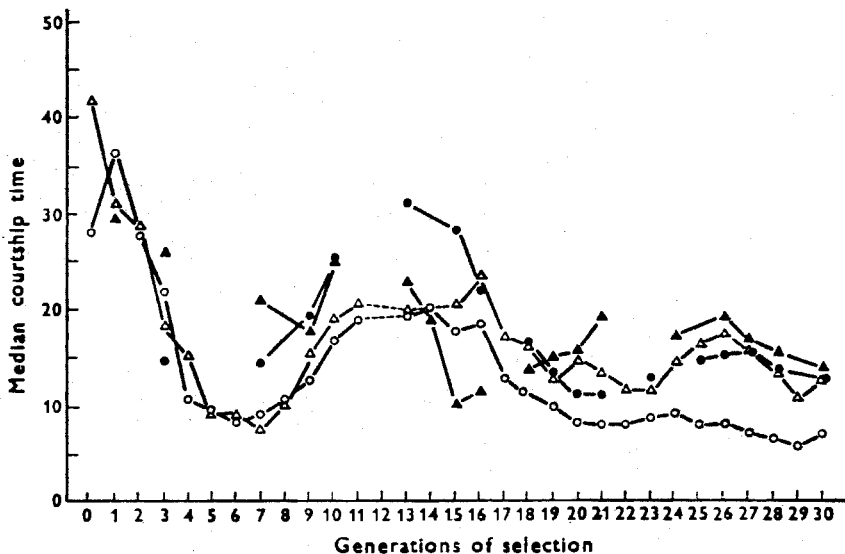


Fig. 3. Three generation moving average for median courtship duration. (Key as Fig. 2.)

VBL 2 is lower than any other line for the last nine generations, and that both selected lines vary less than the controls. Only VBL 2 showed a significant linear trend ( $F=10.50$ ,  $P<0.01$ ).

A more informative procedure is to examine the distribution of courtship times, and to assess changes in this as selection progressed. In this analysis the first 30 min of the observation period only were used. This period was split up into fifteen sub-periods of 2 min, and the number of acceptances falling into each of these sub-periods was calculated. The numbers in each were then transformed to percentages of the total number receptive in the group. The percentages are therefore all independent of the proportional receptivity analysis in the previous section, and may be assessed separately. The percentages were calculated cumulatively.

The first thirty generations of selection for VBL 1 and VBL 2 were split into two sections, each of fifteen generations and the distributions in each of these halves were compared with one another. These are shown in Fig. 4a and b. Since the controls consisted of fewer numbers, each one was analysed as a whole. This is shown in Fig. 4c. It is evident from these graphs, that the two halves of each of the selected lines differ more from one another than do the two control lines.

The data underlying these graphs have been analysed separately, using the Mann-Whitney 'U' Test (Siegel 1956), which confirmed the significance of the shift in the distributions of courtship duration in the second fifteen gener-

ations of selection (VBL1,  $P<0.01$ , VBL 2,  $P<0.001$ ).

### Latency to Courtship

Again the median was used as the measure of central tendency in the analysis of latency. The only trend apparent was in VBL 2, which appeared to have longer latency than the other groups in the later generations of selection.

The first and second fifteen generations were compared, in a manner similar to that in the analysis of courtship duration, and the two selected lines proved to differ in the direction of change. In VBL 1 the latencies for the second fifteen generations were shorter ( $P<0.05$ ), whereas for VBL 2 they become longer ( $P<0.001$ ). It is possible that the decline in latency in VBL 1 was produced artifactually, since this strain had particularly high latencies in the generations affected by mould ( $S_{12}$  and  $S_{14}$ ) which elevated the overall latency for the first fifteen generations.

### Relationship Between Percentage Receptive and Courtship Time: Bi-Dimensional Scaling

Having analysed both percentage receptivity and courtship time independently from one another it is important to assess the relationship between the two, and to investigate whether viewing both variables together gives more information on the progress of selection than either does separately. Also, more idea may be gained as to the biological relationship between these two variables.

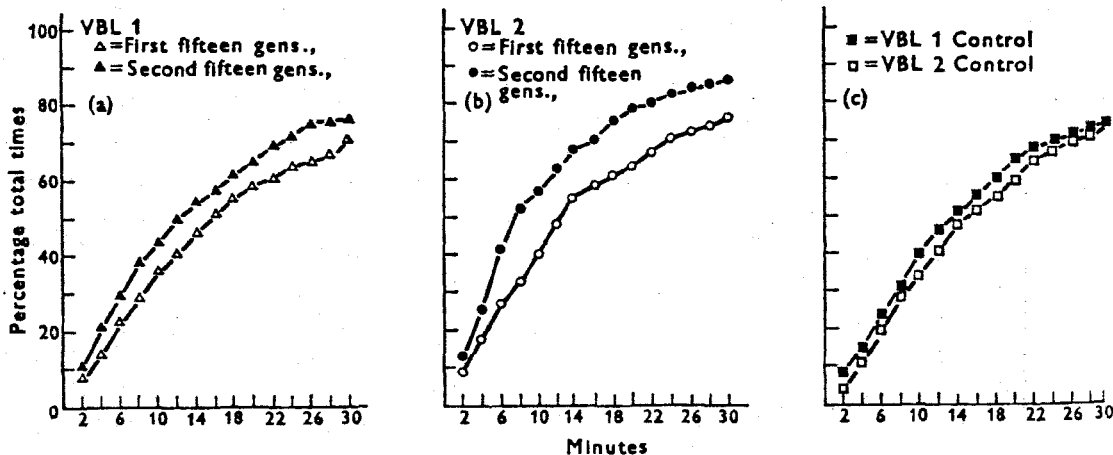


Fig. 4. Comparisons of cumulative distributions of courtship duration.

It is meaningful to correlate these two variables, since it is by no means obvious that there would be an inherent statistical dependency between them. The observation period was of 2 hr and the great majority of the courtship times recorded were well within this; in fact, from the distribution analysis on courtship time, the majority fell within 30 min. Thus it cannot be argued that there is an intrinsic statistical correlation between percentage receptivity and courtship time.

Product moment correlations have been calculated separately for each strain, for both mean and median courtship time with percentage receptivity. They are shown in Table II.

Table II. Experiment 1: Correlations of Mean and Median Courtship Duration with Percentage Receptivity

		<i>r</i>	<i>df</i>	<i>P</i>
VBL 1	Mean	-0.533	27	<0.01
	Median	-0.602	27	<0.01
VBL 2	Mean	-0.551	28	<0.01
	Median	-0.570	28	<0.01

Clearly, the overall tendency is to negative correlation between these variables, and median courtship time correlates slightly better than the mean courtship time, thus vindicating its use as a measure.

Since courtship duration and percentage receptivity are related, probably biologically (Cook 1973), it is possible that a measure of each generation based upon a combination of these variables will show more readily the trends engendered by selection. Unfortunately, no simple means of combining them in one number proved satisfactory. One can, however, plot each generation as a co-ordinate of the two variables, such that the correlation may be seen. If selection has systematically acted upon these variables as a unit, then the points representing the later generations will be shifted further along the correlation axis than those representing the earlier generations.

This shift may be seen in Fig. 5 (a, b, c and d). The data for each of the groups have been segmented into thirds, corresponding to the early, middle and later periods of selection, and plotted using different symbols for each, such that gradual shifts with selection may be perceived. It is difficult to test these trends statistically. Suffice it to say that these graphs portray the relationship between percentage receptivity and

courtship time in a way which is not evident from analysis of either alone. In the VBL 1 graph the squares (last ten generations) tend to cluster in the lower right-hand end of the graph, whereas the circles (first ten generations) are not so prominent here. In VBL 2 this is not so clear since all courtship times tend to be lower. The controls show generally more scatter, and the later generations are mixed among the earlier ones.

## Experiment 2

### Complexity of Character Under Selection

The character under selection is perhaps one of the most complex which has been attempted in behaviour genetics, and selection was imposed as much to elucidate the character itself as to obtain information on its genetic substrate.

The complexity of the character stems from several sources; primarily selection was imposed upon an abnormal behavioural situation, rather than upon an extreme of normal behaviour, as in most selection experiments. It is not even possible at the moment to give precise details of the exact stimulation a female receives from a wingless male, nor to assert definitely that only one of the components of wing vibration (Bennet-Clark & Ewing 1967) is affected. Also, selection was imposed upon both percentage receptivity and courtship time, and the extent of the communality of genetical control of these two variables is not known.

Additionally the adaptation to selection could be a result of changes in either or both sexes. Other data (Cook 1973) show that courtship duration is normally controlled by the female, but in the present situation adaptation on the part of the male might well be an important factor. Part of the increase in courtship time with amputation of the males' wings could be due to lack of persistence in intense courtship by the male after a period of ineffective suit. The manner of his courtship could also change, with behaviours other than wing display assuming a more important role.

It is instructive to ask whether both selected lines have responded in the same fashion. Since the phenotype is complex, there is little reason to suppose that the same changes have occurred in both lines.

If it is true that different adaptations exist then the hybridization of the selected lines should result in a line in which performance is reduced since both adaptations would be broken. On the other hand if the adaptations are similar,

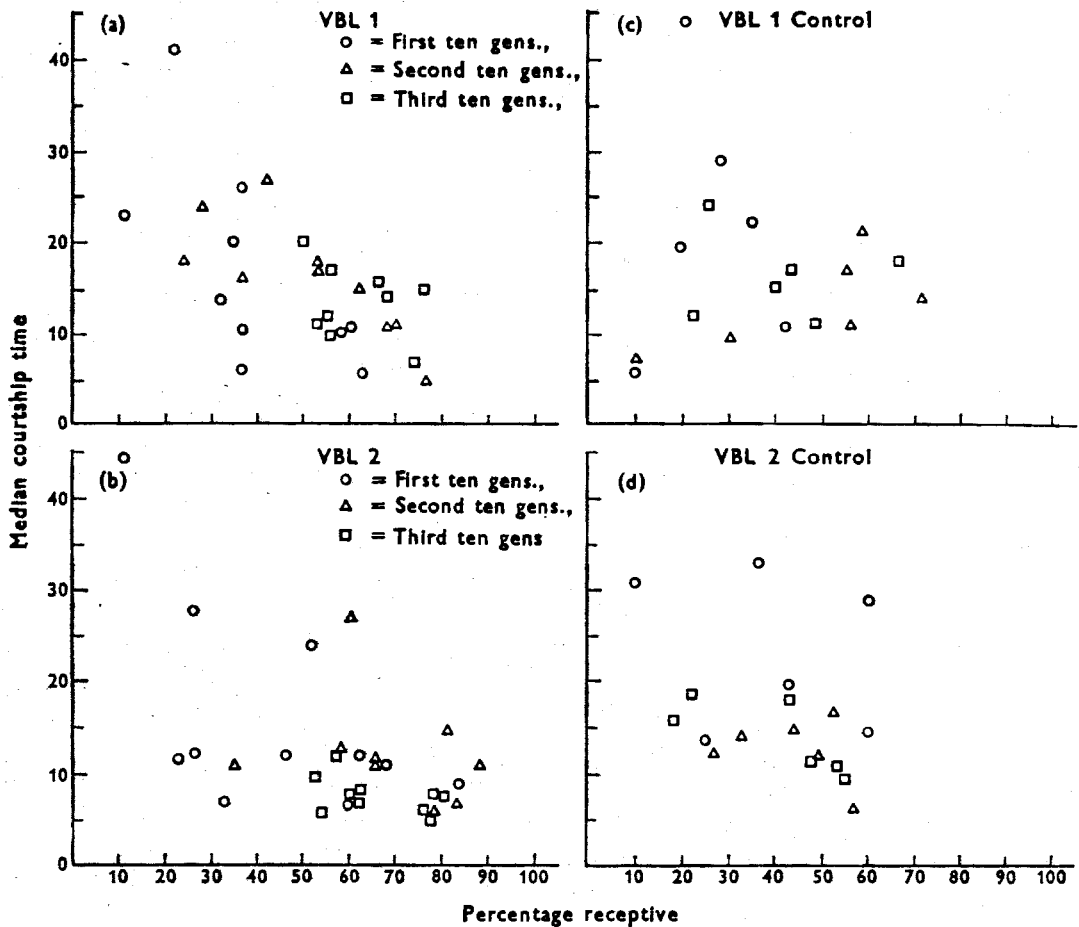


Fig. 5. Relationship between median courtship duration and percentage receptivity.

no such reduction in performance should occur. It is however dangerous to assert these arguments in the absence of information on the genetical control, since not knowing the degree of additivity and dominance of the behaviours concerned makes prediction as to the behaviour of hybrids rather speculative.

Additionally, the procedure will release more genetical variability for selection to act upon. Continuation of selection in the hybrid lines might therefore lead to further selection gains, unless the character is already at some phenotypic 'ceiling'.

#### Methods

The hybridization was conducted at  $S_{31}$ . Crosses were made between the two selected lines, and between the two control lines.

These hybrid lines are called Selx (standing for 'selected cross') and Contx (standing for 'control cross').

The  $F_2$  generation was made from the following parental combinations, upon which the usual selection paradigm was employed:

Selx  $F_2$ —50 per cent males from each of the reciprocal  $F_1$ s of selected origin, and 50 per cent females from each also.

Contx- $F_2$  set up on similar paradigm to Selx.

Subsequent generations were produced under the usual conditions of measurement and selection.

#### Results

##### Percentage Receptivity

The percentage receptivity for Selx and Contx

over the first four generations is shown in Fig. 6, and the data obtained from the parental lines at  $S_{31}$  are also plotted for comparison.

Selx and Contx are consistently separated from one another by at least 30 per cent, and follow identical trends over the four generations. The first two are stable, and are then followed by a steep decline.

It is of particular interest to note that the difference between the means of the two parental lines at  $S_{31}$  is maintained in the hybrid lines.

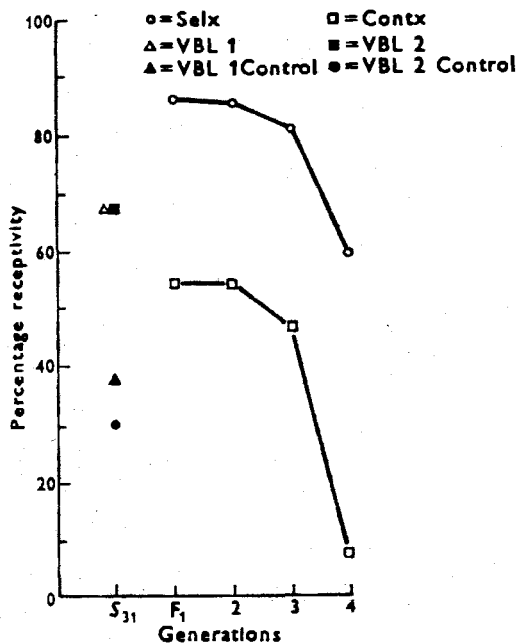


Fig. 6. Percentage receptivity in Selx and Contx,  $F_{1-4}$ .

The difference between the mean of VBL 1 and VBL 2 and that of VBL 1 control and VBL 2 control at  $S_{31}$  is 33.5 per cent. The difference between Selx and Contx at  $F_1$  and  $F_2$  is 32.0 per cent. This implies that the increase in the absolute levels of receptivity in the hybrid lines is probably due to outbreeding, rather than to factors related to the behavioural adaptations in the selected lines.

### Courtship Durations

The mean of the courtship durations from the four generations are plotted in Fig. 7.

Selx is lower than Contx on all but the third generation. Analysis of variance for the case of unequal group sizes (Winer 1962) was applied to this data, a log transform being necessary

to reduce heterogeneity. Only the strains factor was significant ( $F=8.16$ ;  $df=1, 233$ ;  $P<0.01$ ), demonstrating that the selected lines do have lower courtship durations than the control lines. No difference existed for generations, or the interaction of this with strains.

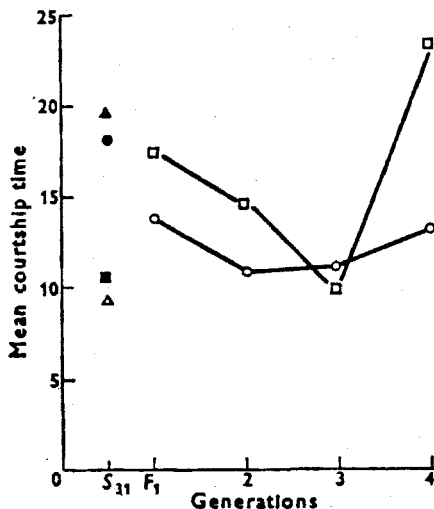


Fig. 7. Mean courtship time in Selx and Contx,  $F_{1-4}$ . (Key as for Fig. 6.)

By comparison with  $S_{31}$  values, one can see that no radical shift has occurred in the levels of courtship duration analogous to that found for percentage receptivity. Both Selx and Contx vary within the ranges set by the parental generation.

### Latency to Courtship

Again the mean latencies are shown graphically in Fig. 8. Apparently the Selx strain has inherited the higher latencies found to be characteristic of the parental strains.

The logarithmic transform reduced  $F_{max}$  below significance in the analysis of variance. The difference between the strains is highly significant ( $F=19.12$ ;  $df=1, 233$ ;  $P<0.001$ ), Selx being longer. No significant difference due to generations was found, but a significant interaction of strains  $\times$  generations did exist ( $F=5.20$ ;  $df=3, 233$ ;  $P<0.01$ ). This is probably due to the high value for Contx at  $F_4$ .

### Experiment 3

Since the aim of the selection experiment was to evaluate the female's response to wingless courtship, it was considered necessary to analyse the receptivity of all female types in one experiment, such that meaningful comparisons could



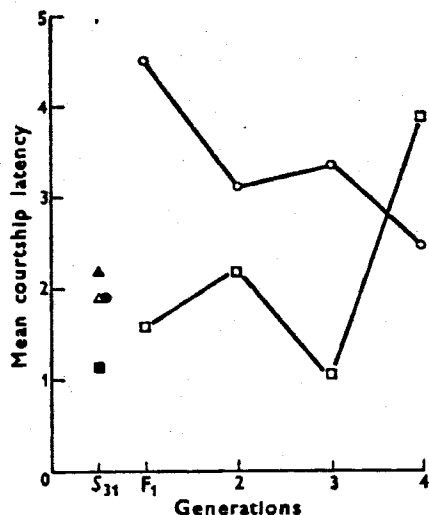


Fig. 8. Mean latency to courtship in Selx and Contx,  $F_1$ -4. (Key as for Fig. 6.)

be made. A design incorporating all the male/female combinations is unfortunately unmanageable since there are six of each type; besides which only broad differences between males are of interest in this context. Consequently, it was decided to use only two types of males in the experiment, one of selected and one of control origin. Measuring all the six female types with these two male types should enable comparison of female receptivity, and broad comparisons of male type.

#### Methods

The six female types used in the experiment were VBL 1, VBL 2, VBL control, VBL 2 control, Selx and Contx. The two types of male were derived as follows:

- (a) *Of selected origin.* These males consisted of 50 per cent mixture of the male progeny from each of the reciprocal crosses of VBL 1 and VBL 2, made at  $S_{31}$ . They are thus effectively  $F_1$  Selx males.

- (b) *Of control origin.* These were produced on a similar paradigm to (a) and the resulting males were effectively  $F_1$  Contx males.

The generation on which the measurement occurred was thus  $S_{32}$  for the original four lines, and  $F_1$  for Selx and Contx.

The measurements were made in the usual way, with male wings amputated on the evening before measurement. The measurement procedure lasted three whole days, and the groups were randomized as to time of day. Fifty pairs per sample were measured, and an observation period of 1 hour was used.

#### Results

##### Percentage Receptivity

Table III shows the percentage receptivity obtained. The 'selected female' half of the matrix is higher in general than the 'control female' half, except for the values for VBL 2. This line underwent a decline in receptivity at this stage in selection. Chi-squared tests have been used to assess the gross differences in proportional receptivity and the values here of them for the tests made are given in Table IV.

The table demonstrates that, with the selected males, the selected females have overall significantly higher percentage receptivity than the control females. There is no significant difference between these types of female when they are with control males. This may be due merely to the inordinately low value for VBL 2 females with control males, since the percentages for the other two selected female types are high.

A significant difference due to male type is only apparent with the selected females, where the selected males are higher.

##### Courtship Duration

Table V contains the means and standard errors of the courtship durations in this experiment. The reduction of heterogeneity by a

Table III. Experiment 3. Percentage Receptivity for All Female Types

Male types	Female types					
	Selected			Control		
	VBL 1	VBL 2	Selx	VBL 1C	VBL 2C	Contx
Selected	80	58	86	64	56	52
Control	62	48	76	52	52	54

Table IV. Experiment 3: Chi-Square Analysis of Proportional Receptivity

Source	Chi-square	df	P
<i>At selected male:</i>			
Selected females pooled × Control females pooled	9.28	1	>0.01
<i>At control male:</i>			
Selected females pooled × Control females pooled	2.30	1	NS
<i>At selected females:</i>			
Selected male pooled × Control male pooled	4.99	1	>0.05
<i>At control females:</i>			
Selected male pooled × Control male pooled	0.49	1	NS

square root transformation enabled analysis of variance, which revealed that only the female factor yields a significant difference ( $F=6.7$ ;  $df=5, 358$ ;  $P<0.01$ ). When the analysis is simplified by pooling within selected type and

control type females it yields an even greater difference on the female factor. Thus it is undoubtedly the case that the selected females have overall shorter courtship times in spite of the high means for VBL 2.

The Mann-Whitney 'U' test was employed to make individual comparisons on the raw data within this matrix. The results confirm that there is no overall difference between the two male types, and that the selected females as a whole had shorter durations than the control females. Pooling across male type it was found that VBL 2 females were significantly longer than both VBL 1 and Selx females ( $Z=3.17$ ;  $P<0.01$  and  $2.35$ ,  $P<0.05$  respectively). Adopting a similar procedure for the controls, the Contx females were significantly longer than the other two control females.

#### Latency to Courtship

Mean and standard error latency are shown in Table VI. Analysis of variance on log latency from this experiment showed that both selected males and selected females were associated with significantly longer latencies than their control counterparts ( $F=9.38$ ;  $df=1, 366$ ;

Table V. Experiment 3: Mean and Standard Error Courtship Duration (minutes)

Male types		Female types					
		Selected			Control		
		VBL 1	VBL 2	Selx	VBL 1 C	VBL 2 C	Contx
Selected	$\bar{X}$	10.59	17.90	13.98	14.12	19.67	28.44
	SE	1.89	2.58	2.38	2.33	3.17	17.80
Control	$\bar{X}$	11.78	17.00	12.27	18.09	13.70	17.81
	SE	2.42	3.36	1.85	2.67	2.04	2.34

Table VI. Experiment 3: Mean and Standard Error Latency (minutes)

Male types		Female types					
		Selected			Control		
		VBL 1	VBL 2	Selx	VBL 1 C	VBL 1 C	Contx
Selected	$\bar{X}$	3.17	2.26	4.50	2.45	1.69	2.42
	SE	0.52	0.36	0.98	0.43	0.54	0.82
Control	$\bar{X}$	2.16	2.60	1.60	1.53	1.97	1.56
	SE	0.37	0.73	0.21	0.32	0.30	0.39

$P < 0.01$ ;  $F = 12.31$ ;  $df = 1, 366$ ;  $P < 0.001$  respectively).

### Discussion

The final experiment has confirmed the overall success of the selection procedure in increasing the percentage receptivity, and reducing the courtship duration, of female *D. melanogaster*. No previous selection experiments with this species, to my knowledge, have reduced courtship duration, even under conditions of normal courtship. Latency to courtship has been reduced (Manning 1961), and courtship duration increased (Manning 1961, 1968; Connolly 1969). This is perhaps because the selection has been upon mating speed as a whole, which allows the adaptation to occur in latency, rather than duration of courtship.

The simplest hypotheses about the broad course of behavioural adaptation under the conditions reported here are that either (a) the female is stimulated by behaviours of the male other than wing vibration, or (b) she is still stimulated by some residual wing vibration, and has developed a means of compensating for its attenuation.

Male *Drosophila* with amputated wings vibrate their stumps in courtship, and according to Waldron (1964) and Ewing (personal communication) produce a signal the characteristics of which are unmodified, although the amplitude is greatly attenuated. On the other hand, the reduction in wing area will virtually remove the component of 'net air movement' shown by Bennet-Clark & Ewing (1967) to be of great importance in stimulating the female. Hypothesis (b) is therefore feasible, and the question becomes one of how the increase in her sensitivity is effected.

One consequence of selection was an overall increase in latency to courtship, which was contributed to by both sexes of the selected animals; this suggests that the factors involved in the initiation of courtship are somehow related to the adaptation in the female's courtship processing system. Manning's (1961) hypothesis concerning the importance of the ability to 'switch' between activity behaviours and sexual behaviours suggests that locomotor activity could be involved in the adaptation, and this question is addressed in the following paper.

### Acknowledgments

I am indebted to the Science Research Council for financial support while conducting this re-

search. Also, I am very grateful to Professor K. J. Connolly for advice and criticism.

### REFERENCES

- Bastock, M. (1956). A gene mutation which changes a behaviour pattern. *Evolution*, **10**, 421-439.
- Bennet-Clark, H. C. & Ewing, A. W. (1967). Stimuli provided by courtship of male *Drosophila melanogaster*. *Nature, Lond.*, **215**, 669-671.
- Bennet-Clark, H. C. & Ewing, A. W. (1969). Pulse interval as a critical parameter in the courtship song of *Drosophila melanogaster*. *Anim. Behav.*, **17**, 755-759.
- Burnet, B., Connolly, K. & Dennis, L. (1971). The function and processing of auditory information in the courtship behaviour of *Drosophila melanogaster*. *Anim. Behav.*, **19**, 409-415.
- Connolly, K. (1969). Spontaneous activity in *Drosophila melanogaster*, its genetic basis and its relationship to other aspects of behaviour. Unpublished Thesis (Ph.D.), University of London.
- Connolly, K. & Cook, R. M. (1973). Rejection responses by female *Drosophila melanogaster*: their ontogeny causality and effects upon the behaviour of the courting male. *Behaviour*, **44**, 142-166.
- Cook, R. M. (1973). Physiological factors in the courtship processing of *Drosophila melanogaster*. *J. Insect. Physiol.*, **19**, 397-406.
- Crossley, S. (1963). An experimental study of sexual isolation within a species of *Drosophila*. Unpublished Thesis (D.Phil.), University of Oxford.
- DeFries, J. C. (1967). Quantitative genetics and behaviour: overview and perspectives. In: *Behavior-Genetic Analysis* (Ed. J. Hirsch), pp. 322-340. New York: McGraw-Hill.
- Ewing, A. W. (1964). The influence of wing area on the courtship behaviour of *Drosophila melanogaster*. *Anim. Behav.*, **12**, 316-320.
- Manning, A. (1961). The effects of artificial selection for mating speed in *Drosophila melanogaster*. *Anim. Behav.*, **9**, 82-92.
- Manning, A. (1967a). The control of sexual receptivity in female *Drosophila*. *Anim. Behav.*, **15**, 239-250.
- Manning, A. (1967b). Antennae and sexual receptivity in *Drosophila melanogaster* females. *Science, N.Y.*, **158**, 136-137.
- Manning, A. (1968). The effect of artificial selection for slow mating in *Drosophila simulans* I. The behavioural changes. *Anim. Behav.*, **16**, 108-113.
- Petit, C. (1958). La détermination génétique et psychophysiologie de la compétition sexuelle chez *Drosophila melanogaster*. *Bull. Biol.*, **92**, 248-329.
- Siegel, S. (1956). *Nonparametric Statistics for the Behavioural Sciences*. Tokyo: McGraw-Hill.
- Sokal, R. R. & Hunter, P. E. (1956). Environmentally caused fluctuations in quantitative characters of *Drosophila*. *Proc. Xth Int. Cong. Entomol.*, **2**, 843-853.
- Sturtevant, A. H. (1915). Experiments on sex recognition and the problems of sexual selection in *Drosophila*. *J. Anim. Behav.*, **5**, 351-366.
- Waldron, I. (1964). Courtship sound production in two sympatric sibling *Drosophila* species. *Science, N.Y.*, **144**, 191-192.
- Winer, B. J. (1962). *Statistical Principles of Experimental Design*. London: McGraw-Hill.

(Received 13 June 1972; revised 25 October 1972; MS. number: 1149)