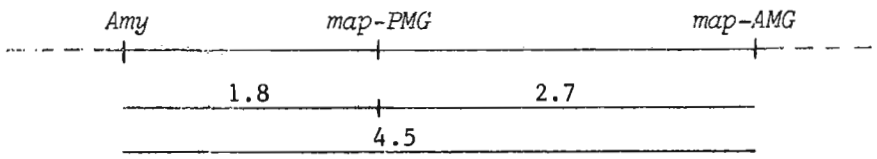
Table 1. Recombination analysis revealing two separable loci, *map-AMG* and *map-PMG*, which control the tissue-specific expression of amylase in the adult AMG and PMG, respectively, in D. melanogaster.

Amy^{1} $map\text{-}AMG^{000}$ $map\text{-}PMG^{00}$ ♀ x $Amy^{1,6}$ $map\text{-}AMG^{123}$ $map\text{-}PMG^{12}$ ♂
(= *iso-CA 1*) (= $Amy^{1,6}$ map^{A})

F_1 ♀ x Amy^{1} $map\text{-}AMG^{000}$ $map\text{-}PMG^{00}$ ♂

Female Progeny

	Amylase	Midgut Pattern	Number (N = 215)
Parental:	1,6	AMG-123, PMG-12	106
	1	AMG-000, PMG-00	102
Recombinant:	1,6	AMG-000, PMG-00	1
	1	AMG-123, PMG-12	2
	1,6	AMG-000, PMG-12	1
	1	AMG-123, PMG-00	3



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References: Abraham, I. and W.W. Doane 1976, Genetics 83:s1; Abraham, I. and W.W. Doane 1978, Proc. Natl. Acad. Sci. USA 75:4446; Doane, W.W. 1969, in RNA in Development, E.W. Hanley, ed., p. 73, Univ. Utah Press, Salt Lake City; Doane, W.W. 1977a, Genetics 86:s15; Doane, W.W. 1977b, J. Cell Biol. 75(2, pt. 2):147a; Doane, W.W. 1978, Int. Conf. Mol. & Devel. Biol. Insects, Crete, Abstracts, p. 45; Powell, J.R. and J.M. Lichtenfels 1979, Genetics, in press.

Espinet, S. and M.L. Tracey. Florida International University, Miami. Detection of differences in the element patterning of D. melanogaster mating behavior.

The difficulties inherent in quantitatively measuring differences in the behavior of Drosophila are well known (Bastock and Manning 1955; Bastock 1956). However, careful description of behaviors, including an account of their patterning in time permits quantification of within and between strain variation. We report a technique in which all possible triplets of behavioral elements which occur at frequencies greater than 1% are graphically overlain to produce a standard sequence. Comparisons of graphical representations indicate both interpopulation and intrapopulation variation.

$X{\cdot}Y^{L}/Y^{S}y+$ males outcompete $X{\cdot}Y^{L}/Y^{S}$yellow males in female choice experiments where all females are $X{\cdot}Y^{L}/X{\cdot}Y^{L}$ ($P<0.001$); and $X{\cdot}Y^{L}y+/Y^{S}$ males outcompete X·/Y males (Tracey and Espinet 1976). To test the hypothesis that the observed differences reflect alterations in the sequence and frequency of courtship elements, pairs of flies were observed and courtship elements were recorded. Recordings were made with a Bell telephone push-button key board coupled

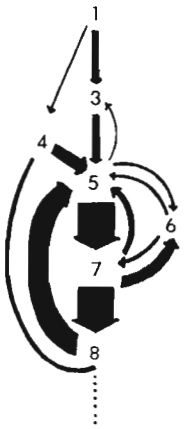
to a 20-pen Esterline-Angus event recorder at chart speeds of 3.8-4.0 cm per minute. Twenty elements were recorded, but some were eliminated by the 1% triplet criterion employed. Those involved in the final analysis were: (1) male standing approximately 1 mm directly behind female, (2) female preening, (3) male scissoring, (4) male following female, (5) male vibrating, (6) male circling female, (7) male licking female's genitalia, (8) male abdomen curling or attempted copulation. Note that successful mating did not always follow attempted mating; compare T(X-Y),yellow and T(X-Y),y+ in Fig. 1. Courtship behavior was identified as the sequence of elements preceding successful copulation. Thus a shift from more or less passive behaviors such as walking to active alteration was used to define the onset of courtship.

The frequencies of all possible combinations of triplets of behavioral elements were calculated. Triplets of elements that occurred at a frequency less than 0.01 were eliminated from the analysis for each trial. The normalized probability for each triplet of elements in a trial was obtained by setting the sum of the frequencies of each element triplet observed more often than one in 100 equal to 100%. Since only two of the recording sessions involving Xy+.//Y males terminated in successful copulation two trials of recordings from each of the

Figure 1. Temporal pattern and element triplet performance probabilities of courtship behaviour in T(X-Y),*yellow*, T(X-Y),*y+* and X·-Y,*y+* *Drosophila melanogaster* stocks. Behavioural elements are represented numerically (see text for descriptions); sequences of triplets are listed in the first column of each study, followed by their associated probability of performance (P). Triplets having observed frequencies of less than 0.01 are not included. Diagrams of the probable sequences of performance of courtship behaviour elements for each pair of flies are presented. The probability that one behavioural element is followed by another is indicated by the width of the arrows.

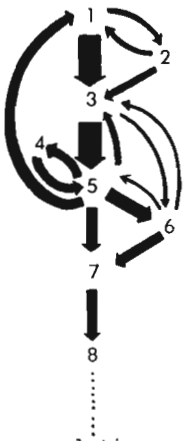
T(X-Y), *yellow*

Sequence		P
1.	5,7,8	0.282
2.	8,5,7	0.189
3.	7,8,5	0.109
4.	4,5,7	0.080
5.	5,7,6	0.057
6.	1,3,5	0.051
7.	5,7,5	0.045
8.	7,8,4	0.038
9.	7,5,7	0.034
10.	5,6,7	0.028
11.	8,4,5	0.022
12.	1,4,5	0.017
13.	6,5,3	0.017
14.	6,7,5	0.017
15.	6,7,8	0.017



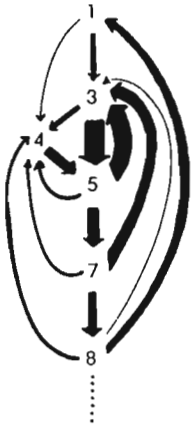
T(X-Y),*y+*

Sequence		P
1.	1,3,5	0.173
2.	3,5,6	0.103
3.	5,1,3	0.080
4.	5,7,8	0.075
5.	5,6,7	0.072
6.	5,4,5	0.070
7.	2,3,5	0.066
8.	5,3,5	0.062
9.	6,7,8	0.060
10.	4,5,4	0.056
11.	4,5,7	0.044
12.	1,2,1	0.044
13.	3,5,1	0.035
14.	6,5,7	0.020
15.	6,3,5	0.020
16.	3,6,7	0.019



X·-Y,*y+*

Sequence		P
1.	5,3,5	0.193
2.	3,5,3	0.162
3.	5,7,3	0.120
4.	4,5,7	0.115
5.	7,8,1	0.058
6.	3,5,7	0.051
7.	7,3,4	0.050
8.	1,3,5	0.048
9.	5,4,5	0.043
10.	7,4,5	0.036
11.	8,4,5	0.036
12.	5,7,4	0.028
13.	3,4,5	0.028
14.	1,4,5	0.022
15.	8,3,5	0.011



three males were analyzed and the within-strain data pooled to obtain an average probability of performance for each triplet of elements. The results are presented in Fig. 1.

The standard sequence of behavior in X·/Y,y+ males is 1→3→5→7→8. In the event the "next" element is not elicited at any point in the sequence, interruption results in the individual starting again at the initial elements (1, 3 or 4) of the sequence. The triplet sequence 3→5→7 is most frequent and perhaps most important in the behavioral repertoire of these males. It should be noted that circling (6) does not play an important role in the mating behavior of these males (Manning 1955).

In T(X-Y)y+, circling plays a more significant role; 1→3→5→6→7→8 is the standard sequence in this case. The initial elements of the sequence are more frequently elicited when these males are wild body-colored, and female preening (2) appears to stimulate male scissoring. When males are yellow, male scissoring is not affected by element 2, and circling (6) does not fit as neatly into the standard sequence as it does in y+ bearing males. The standard sequence in the case of T(X-Y) yellow males is 1→3→5→7→8 with the subset 5→7→8 being most frequently elicited.

These results are consistent with the threshold theory of behavioral elicitation, where each behavioral element in the sequence has a higher threshold than the element directly preceding it. In the event this threshold level of stimulation is not achieved the particular behavioral element is not elicited; rather a preceding element with a lower threshold appears in the sequence (Bastock 1956).

References: Bastock, M. and A. Manning 1955, Behavior 8:7-111; Bastock, M. 1956, Evolution 10:84-92; Manning, A. 1965, Viewpoints in Biology 4:125-169; Tracey, M.L. and S.A. Espinet 1976, Nature 263:321-323.

Fadda, S., S. Sangiorgi and E. Pieragostini. Istituto di Genetica, Universita di Bologna, Italy. G6PD electrophoretic phenotype variation during development of D. melanogaster laboratory populations.

Developmental pattern of G6PD isozymes in D. melanogaster was investigated from egg deposition up to the 48th hour by Wright and Shaw (1970). When they crossed parents exhibiting different electromorphs, F_1 embryos showed both maternal and paternal forms of the enzyme by the 23rd hour; they concluded that genetic and molecular models, proposed for adult G6PD (Young et al. 1964; Steele et al. 1968), could hold also for the developmental expression of the enzyme.

This does not seem to be the case in our lab populations: when investigated through electrophoresis of mass homogenates, they exhibited different electrophoretic phenotypes, that did not reflect adult variation nor were inherited following any simple Mendelian scheme (Pieragostini et al. 1978; Fadda et al. 1979).

These observations agree with a good deal of evidence about complex determination of G6PD in D. melanogaster adults of our populations (Pieragostini et al. 1978) and others studied by several authors (Komma 1968; Giesel 1976). With the present communication we complete the picture of G6PD developmental polymorphism through electrophoretic observations of two day old pupae and discuss them in relation to larval and adult stages.

We sampled pupae from Canton strain, from an unrelated strain carrying the vg marker and from six populations having a Canton x vg cross as their common origin, plateaued for a quantitative trait after about 70 generations of selection (Palenzona and Alicchio 1973). We maintained these populations in mass culture at 25°C for several generations and then took random samples of about 100 individuals in the proper developmental phase. Cellogel electrophoresis was carried out on multiple homogenates of the above samples, following the procedure detailed in Pieragostini et al. 1978. We also calculated experimental errors affecting relative mobilities in order to base our homology statements upon statistical testing. For all cases where we suspected the existence of mobility differences, we examined electrophoretically mixed samples and took single band patterns as evidence of homology.

The results obtained analyzing electrophoretically our lab populations are presented in Fig. 1, which summarizes published observations of adult samples (from Pieragostini et al. 1978), of larval samples (Fadda et al. 1979) and original data from pupal samples. In general, we may point out that both larval and adult stage exhibit several differences between populations, while pupal stage has a single variant common to all populations (Fig. 2); however, the pupal electromorph is slower than any other observed variant.

For larval stage in particular it is worth noticing that the variants from parental populations (Canton and vg) disappear in the progeny (selected lines), where bands of intermediate mobility are present; parental variants of adult stage behave differently, because they are maintained in the progeny and are rearranged in patterns typical of vg and winged populations. Since genetic analyses, performed on each of the two stages separately (Fadda et al. 1979 for larvae; Pieragostini et al. 1978 for adult flies), provided evidence that these variants are not inherited in simple Mendelian fashion, the authors suggested regulatory hypotheses for these phenomena. However, as these phenomena exhibit no similarities in larval and adult stages, we might add to the regulatory hypothesis that the mechanisms controlling the expression of adult and larval variants depend on the specific developmental stage, whether the structural genes are the same or not.

As for the pupae, they seem to differ "non-specifically", that is, depending on the very developmental stage rather than on the genetic complement of each population. We suggest the expression of pupal G6PD to depend on the physiological state, either because the electromorph actually has a peculiar function in pupal metabolism, or because it is modified as a metabolic side effect. Examples of such epigenetic developmental variation, due to modifiers present in