A MERISTIC TRAIT IN *DROSOPHILA MELANOGASTER* × *SIMULANS* HYBRIDS

J. D. AGNEW (1973)

Department of Genetics, University of the Witwatersrand,
Johannesburg, South Africa

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A quantitative trait, abdominal bristle number, is described in a number of stocks of the two sibling species *Drosophila melanogaster* and *Drosophila simulans* and in interspecific hybrids obtained from these stocks. Coefficients of variation for the trait in the parental species and the hybrids are compared, and in the case of the latter are found to fall in the same range as those of the pure species. The results are discussed in the light of previous findings on other bristle systems.

Introduction

Drosophila melanogaster Meigen 1830 and *Drosophila simulans* Sturtevant 1919 are a pair of sibling species within the *melanogaster* species group of subgenus *Sophophora*. This species group has recently been reviewed by BOCK and WHEELER (1972). Both species appear to be widespread in southern Africa, as well as other areas of Africa, and are of special interest to the student of evolution because, although they are genetically completely isolated from each other by means of a hybrid sterility barrier, there is incomplete sexual isolation. MOURAD and MALLAH (1960) found that under natural conditions some hybridization does take place, and SPERLICH (1962) found, on the island of Lipari (S. Italy), that five percent of the females caught "gave only sterile female offspring of a typical appearance, most probably resulting from the cross *D. melanogaster* female × *D. simulans* male." Thus, under natural conditions, the frequency of interspecific matings, where the two species are co-existent, can be surprisingly high.

In the laboratory, the two species can be induced to hybridize with moderate facility, as a number of reports has established. During the last few years, a laboratory study was made of the sexual isolation between various populations of these two species. The populations

had been kept for a number of years as laboratory stocks, and originated from various parts of southern Africa. As a result of this work, a considerable number of hybrids were produced between compatible or interfertile strains, and most of these were routinely stored for later study. As the number of hybrids recovered represents a fair sample, it was possible to describe the variation in a quantitative trait in the hybrids, and it is this aspect of the work that is reported in the present paper.

Material and Methods

STOCKS

The stocks used to generate the hybrids are listed in Tables 1 and 2, together with the dates and places of collection, and the abbrevia-

TABLE 1
STOCKS OF *D. MELANOGASTER* USED

Locality of collection	Stock symbol	Date
1. Inhaca Island, Moçambique	Inh-1	1947
2. Magaliesberg, Transvaal	Mag-1	1961
3. Graaff-Reinet, Cape	GR-1	1949
4. Bloemfontein, O.F.S.	Bfn-1	1959
5. Zoutpansberg, N. Transvaal	Zpb-1	1947
6. Nelspruit, E. Transvaal	Ne-1	1947
7. Witwatersrand, Transvaal	WWR-63	1963
8. Cape Town, Cape	CT-1	1948
9. Stellenbosch, Cape	ST-2	1954
10. Johannesburg, Transvaal	WWR-2	1944
11. Bethulie, O.F.S.	Beth	1959
12. Lake Nyasa, Malawi	Ny-1	1961
13. Drakensberg, Natal	Drak	1961
14. Port St. Johns, Transkei	UR-1	1959
15. Cedara, Natal	CED-2	1947
16. Inhaca Island, Moçambique	Inh-6	1957
17. Stanford Lake, Transvaal	SL	1957
18. Lake Nyasa, Malawi	Ny-1X	1961
19. Inhaca Island, Moçambique	Inh-4	1958
20. Angola (locality not known)	An	1967
21. Kalahari, N. Cape	Ka-1	1961

TABLE 2
STOCKS OF *D. SIMULANS* USED

Locality of collection	Stock symbol	Date collected
1. Umngazi River near Port St. Johns, Transkei	UR	1959
2. Mkuzi Game Reserve, Natal	Mk-1	1947
3. Zoutpansberg, N. Transvaal	Zpb-5	1952
4. Krugersdorp, S. Transvaal	WWR-6	1955
5. Inhaca Island, Moçambique	Inh-1	1957
6. Drakensberg, Natal	Drak	1958
7. Bethulie, Orange Free State	Beth	1959

tions used to code the stocks. The stocks were founded from small samples of adults caught in the wild.

Stock cultures were maintained on the usual cornmeal-molasses-syrup-agar food, fortified with yeast and inoculated with live yeast. Cultures were kept at $25^{\circ}\text{C} \pm 1^{\circ}\text{C}$, in small-scale mass culture, in clear glass bottles of 300 ml capacity; each stock was kept in duplicate and transfers to fresh food took place every three to four weeks.

A few of the stocks were accidentally lost during the period they were under study. These were the *D. melanogaster* stocks CED-2, which was lost in March 1970 and Inh-6 which was lost in October 1971. The stock CED-2 was lost before it could be tested to completion for interfertility with *D. simulans*.

METHODS

For bristle counts, a sample of a few hundred individuals of each stock was etherized and placed in preservative (isopropanol 50, water 44, glacial acetic acid 5, glycerol 1). It was found to be easier to count the bristles with the specimens preserved in fluid. The sample was labelled, dated and kept for later checking if necessary. In each stock, twenty females and twenty males were scored for bristle number on the fourth and fifth abdominal sternites, that is 4S and 5S in the terminology of *Drosophila* morphology (DEMEREK 1965). Abdominal bristle number is the total of 4S plus 5S. In the case of the hybrids, where in many cases fewer than twenty offspring were recovered, only those bottles yielding more than twenty offspring of one sex

are recorded here; where larger numbers were recovered, samples of twenty were scored and this was possible because most specimens excepting those used for attempted backcrosses were kept in preservative. In a number of successful crosses, however, the hybrids recovered were inadvertently either not kept or lost, so that the tables showing the hybrids (Tables 7 and 8) do not record the full position regarding interfertility between all stocks of the two species.

HYBRIDIZATIONS

Hybridization bottles were set up using ten unfertilized females of one strain and ten males of the other species ("no-choice method"). Parents were removed from the bottles after a week, and kept preserved for checking purposes afterwards. All possible combinations of the two species, including the reciprocal crosses, were made. Due to failure of some of the hybridization bottles, mainly false positives because of the accidental use of non-virgin females, certain crosses had to be repeated. It would appear that, in the case of *D. simulans*, females in the stock bottles are fertilized very soon after emergence, as was remarked by MORGAN (1929). Crosses were numbered consecutively, and from cross number 115 onwards, the collection of virgin females was abandoned. Instead, final instar larvae which had left the culture medium to pupate on the sides of the bottle were collected and sexed by examination of the larval gonad. In this way, crosses could be made at any time of day without the necessity of clearing stock bottles of flies. As before, when this method was used, ten larvae of one sex and from one stock were placed on fresh food with ten larvae of the opposite sex from an appropriate stock of the other species. In some of the crosses after cross number 115, only female larvae were selected. When these emerged as adults, male imagines of the appropriate stock and species were added. When using alien males, the age of the females seems to play some part in the success or otherwise of the cross. In all, 342 hybridization bottles were set up to cover all combinations of the two species.

Results

QUANTITATIVE CHARACTER

The character studied was abdominal bristle number, as defined in the previous section; this is a meristic or countable character which has been widely studied in quantitative genetics, beginning with the work of MATHER (1941), and MATHER & HARRISON (1949). These workers showed that the trait was under polygenic control, in fact, regulated by balanced polygenic combinations, subject to an internal balancing process in homozygotes and a relational balancing process in heterozygotes. Polymorphism was accounted for in terms of the relative efficiency of the internal and relational balances. Later, HARRISON & MATHER (1950), by means of selection experiments, postulated a minimum of ten genes to account for their results but qualified their conclusions by stating that it is "very unlikely that the number is in fact as low as this minimum."

A number of studies on this trait has since appeared. CLAYTON & ROBERTSON (1957) were interested in estimating the heritability of the trait and found, using offspring-parent regression, that it was approximately 0.5; using half-sib and full-sib correlation, it was 0.48 and 0.52 respectively. SHELDON (1963) using selection differentials found heritability to be somewhat lower, about 20-25 percent. WERKMEISTER (1967) estimated it to be 0.26, while RASMUSON (1964) found it to be about 0.5 in one selection line and 0.3 in another. The last-mentioned author postulated 30-36 effective factors for abdominal bristle number. SHERIDAN et al. (1968) have studied the partitioning of variance for different bristle systems and estimate heritability of the trait at 0.28 to 0.35.

All the above-mentioned studies have reported on *D. melanogaster* only. The character was accordingly measured in all stocks of *D. melanogaster* and *D. simulans* available and the hybrids where these were obtained.

ESTIMATED PHENOTYPIC PARAMETERS FOR THE BASE POPULATIONS

Counts were made on each stock of the parental species as described in the section on methods; counts were repeated approximately one

year later, the years being 1968 and 1969. The results (1968 data) are given for *D. melanogaster* in Tables 3 and 4, and for *D. simulans* in Tables 5 and 6. The Tables show mean bristle number and variance for each stock; this adequately describes the trait in each stock since MATHER (1941) has shown that, for this trait, the frequency distribution curves approximate to normality and are typical of the frequency distributions observed for polygenically controlled characters in general.

TABLE 3
ABDOMINAL BRISTLE NUMBER IN FEMALES OF *D. MELANOGASTER*:
MEANS AND PHENOTYPIC VARIANCES

Stock		Mean $\pm$ std. error	Variance
<i>D. melanogaster</i>	Inh-1	37.85 $\pm$ 0.53	5.53
"	Mag-1	34.30 $\pm$ 0.58	6.81
"	GR-1	47.65 $\pm$ 0.48	4.63
"	Bfn-1	47.35 $\pm$ 0.60	7.13
"	Zpb-1	44.75 $\pm$ 0.45	4.09
"	Ne-1	45.30 $\pm$ 0.87	15.21
"	WWR-63	34.90 $\pm$ 0.54	5.89
"	CT-1	43.40 $\pm$ 1.46	42.84
"	ST-2	40.20 $\pm$ 0.81	13.16
"	WWR-2	44.35 $\pm$ 1.07	22.83
"	Beth	37.80 $\pm$ 0.86	14.66
"	Ny-1	37.35 $\pm$ 0.53	5.63
"	Drak	31.05 $\pm$ 0.78	12.25
"	UR-1	33.85 $\pm$ 0.70	9.83
"	CED-2	39.60 $\pm$ 0.77	11.99
"	Inh-6	34.55 $\pm$ 0.74	10.95
"	SL	43.05 $\pm$ 0.85	14.55
"	Ny-1X	40.85 $\pm$ 0.64	8.23
"	Inh-4	41.10 $\pm$ 0.38	2.89
"	An	45.55 $\pm$ 0.87	15.15
"	Ka-1	39.00 $\pm$ 0.57	6.60

In Tables 4 to 6, only the results for the first set of samplings is given; a year later much the same picture is apparent, but some random fluctuations in mean bristle number do occur and this is possibly due to sampling errors introduced when transfers of the cultures take place. Nevertheless, the coefficients of variation, which are not presented in tabular form but are discussed further below,

TABLE 4

ABDOMINAL BRISTLE NUMBER IN MALES OF *D. MELANOGASTER*:
MEANS AND PHENOTYPIC VARIANCES

Stock		Mean $\pm$ std. error	Variance
<i>D. melanogaster</i>	Inh-1	30.10 $\pm$ 0.37	2.79
"	Mag-1	30.15 $\pm$ 0.55	6.03
"	GR-1	37.00 $\pm$ 0.50	4.90
"	Bfn-1	36.55 $\pm$ 0.57	6.55
"	Zpb-1	37.15 $\pm$ 0.58	6.73
"	Ne-1	35.45 $\pm$ 0.73	10.55
"	WWR-63	30.25 $\pm$ 0.76	11.39
"	CT-1	33.85 $\pm$ 0.84	14.03
"	ST-2	31.95 $\pm$ 0.42	3.45
"	WWR-2	32.50 $\pm$ 0.76	11.45
"	Beth	29.10 $\pm$ 0.85	14.39
"	Ny-1	29.70 $\pm$ 0.48	4.61
"	Drak	24.40 $\pm$ 0.75	11.24
"	UR-1	27.35 $\pm$ 0.58	6.73
"	CED-2	31.51 $\pm$ 0.48	4.63
"	Inh-6	29.10 $\pm$ 0.61	7.39
"	SL	35.50 $\pm$ 0.49	4.85
"	Ny-1X	35.30 $\pm$ 0.61	7.41
"	Inh-4	32.70 $\pm$ 0.50	4.91
"	An	38.60 $\pm$ 0.99	19.24
"	Ka-1	31.30 $\pm$ 0.53	5.61

TABLE 5

ABDOMINAL BRISTLE NUMBER IN FEMALES OF *D. SIMULANS*:
MEANS AND PHENOTYPIC VARIANCES

Stock		Mean $\pm$ std. error	Variance
<i>D. simulans</i>	UR	34.30 $\pm$ 0.61	7.41
"	Mk-1	34.40 $\pm$ 0.75	11.14
"	Zpb-5	37.70 $\pm$ 0.64	8.31
"	WWR-6	31.30 $\pm$ 0.77	11.91
"	Inh-1	32.90 $\pm$ 0.54	5.89
"	Drak	33.30 $\pm$ 0.83	13.91
"	Beth	36.50 $\pm$ 0.60	7.15

TABLE 6

ABDOMINAL BRISTLE NUMBER IN MALES OF *D. SIMULANS*:
MEANS AND PHENOTYPIC VARIANCES

Stock		Mean $\pm$ std. error	Variance
<i>D. simulans</i>	UR	27.90 $\pm$ 0.61	7.39
"	Mk-1	29.15 $\pm$ 0.52	5.33
"	Zpb-5	28.55 $\pm$ 0.46	4.15
"	WWR-6	25.30 $\pm$ 0.71	10.11
"	Inh-1	27.55 $\pm$ 0.48	4.55
"	Drak	25.40 $\pm$ 0.48	4.54
"	Beth	29.95 $\pm$ 0.48	4.55

are much the same in all stocks, varying from a low of around five percent to a high of fifteen percent, with most stocks having coefficients of between six and ten percent.

In the case of *D. melanogaster* (Tables 3 and 4), it will be seen that the different stocks have different means, suggesting that they are characterised by different combinations of genes. In all cases, females have a higher mean than males for a particular stock; means for females vary from a low of 31.05 to a high of 47.65, the corresponding figures for males being 24.40 and 38.60. There is some overlap of female and male bristle number among the stocks. It may be noted that some of the stocks originate in a common locality, for example, Inh-1, Inh-4 and Inh-6 are all from Inhaca Island, Moçambique; WWR-2 and WWR-63 from the Witwatersrand area; Ny-1 and Ny-1X from Malawi. In all cases the stocks from a particular station or area show significantly different bristle numbers.

In the case of *D. simulans* (Tables 5 and 6), bristle number in this species is somewhat lower than in *D. melanogaster*, although there is some overlap between the two species. There is, however, no overlap between the sexes as there was in *D. melanogaster*. Mean female bristle number is always higher than the male number, in every stock; whether this always holds, will depend on examination of a greater number of stocks of *D. simulans*. The different mean values for the various stocks suggest that this species is also polymorphic for bristle genes, each stock having a different combination, fluctuating over time due to environmental influences and drift of gene frequencies.

THE TRAIT IN HYBRIDS

The data for the male hybrids are presented in Table 7, and those for the female hybrids in Table 8; both tables also show the parental combinations which were successful in generating more than ten hybrids, and which could be used for statistical purposes. The in-

TABLE 7

MALE HYBRIDS OF *D. MELANOGASTER* × *D. SIMULANS*:

MEANS AND VARIANCES OF BRISTLE NUMBER

s = *D. SIMULANS*; m = *D. MELANOGASTER*

Cross No.	Parents used:			Mean ± std. error	Variance
	♀	×	♂		
1	s UR	×	m ST-2	29.65 ± 0.84	14.02
2	s UR	×	m GR-1	29.80 ± 0.63	7.85
3	s UR	×	m Bfn-1	27.75 ± 0.59	6.99
4	s UR	×	m Zpb-1	28.30 ± 0.67	8.91
5	s UR	×	m Drak	28.65 ± 0.59	6.93
14	s Inh-1	×	m Inh-1	28.91 ± 0.39	1.66
15	s Inh-1	×	m GR-1	30.75 ± 0.65	8.39
19	s Beth	×	m GR-1	33.29 ± 0.74	9.20
29	s UR	×	m WWR-63	26.10 ± 0.59	6.99
30	s Beth	×	m SL	32.80 ± 0.70	9.75
31	s Beth	×	m Ne-1	34.75 ± 1.04	21.68
226	s Beth	×	m Drak	29.67 ± 0.76	6.97
228	s Beth	×	m An	29.20 ± 0.61	7.57
230	s Drak	×	m An	27.55 ± 0.81	13.14
238	s Beth	×	m CT-1	32.00 ± 0.87	13.99
239	s Drak	×	m Drak	25.10 ± 0.69	9.48
240	s Drak	×	m SL	26.25 ± 0.44	3.94
241	s Drak	×	m Zpb-1	28.20 ± 0.69	9.46
286	s Inh-1	×	m ST-2	28.30 ± 0.63	7.91
294	s Inh-1	×	m Inh-4	27.82 ± 0.56	5.25
321	s UR	×	m Inh-1	28.45 ± 0.51	5.15
323	s UR	×	m Ne-1	31.18 ± 0.69	8.03
327	s UR	×	m CT-1	27.10 ± 0.49	4.89
329	s UR	×	m Beth	27.90 ± 0.64	8.07
330	s UR	×	m Ny-1	26.25 ± 0.51	5.19
332	s UR	×	m SL	27.30 ± 0.37	2.81
334	s UR	×	m Inh-4	27.90 ± 0.49	4.79
338	s Drak	×	m WWR-2	26.10 ± 0.68	9.20
340	s Zpb-5	×	m WWR-2	27.20 ± 0.71	10.02
342	s Drak	×	m CT-1	31.65 ± 0.54	5.82

TABLE 8
FEMALE HYBRIDS OF *D. MELANOGASTER* × *D. SIMULANS*:
MEANS AND VARIANCES OF BRISTLE NUMBER
s = *D. SIMULANS*; m = *D. MELANOGASTER*

Cross No.	Parents used:			Mean ± std. error	Variance
	♀	×	♂		
15	m Inh-1	×	s GR-1	40.00 ± 0.75	5.61
26	m SL	×	s Inh-1	42.10 ± 0.58	6.68
41	m Ny-1	×	s WWR-6	39.63 ± 1.37	35.95
126	m An	×	s UR	44.20 ± 1.01	20.45
128	m An	×	s Drak	46.00 ± 0.63	7.77
129	m An	×	s Beth	47.60 ± 0.89	15.76
131	m Ne-1	×	s Beth	46.85 ± 0.92	17.04
136	m CT-1	×	s Inh-1	46.30 ± 0.60	7.24
144	m ST-2	×	s Mk-1	43.50 ± 0.61	7.56
145	m ST-2	×	s Inh-1	43.95 ± 0.66	8.75
146	m ST-2	×	s Beth	45.80 ± 0.76	11.55
148	m CT-1	×	s Drak	45.35 ± 0.58	46.95
149	m CT-1	×	s Beth	48.50 ± 0.49	4.74
155	m Drak	×	s Inh-1	40.55 ± 0.33	2.14
156	m Drak	×	s Drak	39.55 ± 0.56	6.35
157	m Drak	×	s Beth	43.35 ± 0.58	6.61
162	m Ny-1X	×	s WWR-6	45.30 ± 0.55	6.12
163	m Ny-1X	×	s Inh-1	44.95 ± 0.73	2.13
172	m Ka-1	×	s WWR-6	42.35 ± 0.91	16.42
178	m Inh-4	×	s UR	42.95 ± 0.55	5.95
181	m Ne-1	×	s Mk-1	45.50 ± 0.53	5.55
182	m Ny-1X	×	s Mk-1	46.70 ± 0.57	6.41
183	m Inh-4	×	s Mk-1	46.55 ± 0.61	7.34

variable sterility of the hybrids precludes a formal genetic analysis on a comparative basis between the two species.

Discussion

STURTEVANT (1920, 1921a, 1921b) was the first worker to have successfully hybridized the two species; he studied the dorsocentral bristles of the hybrids and found that bristles were often lacking. For example, the pure *melanogaster* and *simulans* parents had coefficients of variability for the dorsocentrals of 3.63 and 0.05 respectively, while the hybrid offspring showed a coefficient of 52.60, a

reflection of the many missing bristles. Sturtevant concluded that the various bristle peculiarities found in the hybrids but not in the parental species, must be due to complementary genes carried by the two species.

Later BIDDLE (1932) made a thorough study of the bristles of hybrids between *melanogaster* and *simulans*. The bristle systems studied were the dorsocentrals and the scutellars, and a wide spectrum of stocks was used to generate hybrids. Biddle found that about fifty percent of the hybrids have bristles missing, and that different stocks differ in this effect, the differences being chromosomal rather than cytoplasmic in origin. It was also found that male hybrids show the bristle effect more than do female hybrids.

Soon afterwards, SCHULTZ & DOBZHANSKY (1933) produced triploid hybrids by crossing 3N *melanogaster* females with 2N *simulans* males. This cross produced diploid females, triploid females and intersexes, the triploid hybrids having two sets of *melanogaster* chromosomes and one set of *simulans* chromosomes. It was found that in the triploid hybrids the normal complement of bristles was present, whereas the diploids from the same parents showed missing thoracic bristles. Schultz & Dobzhansky concluded that "apparently among the complementary genes involved in the bristle disturbance, some of those introduced from *simulans* are recessive to two of their *melanogaster* allelomorphs."

In order to compare the bristle data derived from the parental populations with that of the hybrids, variation coefficients for each stock and each batch of hybrids were computed. The frequency distributions of these coefficients are displayed graphically in Figure 1.

The coefficients of variation in the hybrids fall within the range recorded for the parental species, and an increase in the coefficient is not seen, as would occur if there were extra bristles or bristles missing. From Figure 1 it is apparent that male hybrids, on the overall picture, have marginally higher coefficients of variation than do the female hybrids, thus falling into line with BIDDLE's (1932) finding that the male hybrids show the bristle effect more than do female hybrids. In the case under discussion, one can scarcely speak of a bristle effect, as the hybrid values are within the range of the parental values and no disturbances are apparent.

The results reported here suggest that the parental genomes form

Fig. 1. Frequency distributions of variation coefficients for bristle number in stocks of *D. melanogaster* and *D. simulans* and their hybrids. Arrow indicates the median of each histogram; n = number of samples where each sample is 20 individuals for the species, and between 10 and 20 for the hybrids.

a compatible or harmonious combination for abdominal bristle formation in the hybrid zygote, and it is possible that the set of polygenes controlling this character is virtually identical in number in the two species and almost entirely allelic in nature. Thus, in contrast to the other bristle systems studied in hybrids, no detectable divergence in the genetic basis for abdominal bristle number has occurred since the two species diverged from a common stem. It may be noted that JONES *et al.* (1969), on the basis of selection experiments for increased abdominal bristle number, found that there was no correlation between scutellars and abdominals, thus demonstrating the genetic independence of the two systems; DAVIES (1971), found that all genes affecting sternopleural bristle number were separable from all genes affecting abdominal bristle number.

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