

## DARWINIAN FITNESS IN *Drosophila*. III. FITNESS COMPONENTS OF *Drosophila sturtevantii*\*

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### ABSTRACT

This is a study of 28 fitness components of 16 chromosomal constitutions of *Drosophila sturtevantii* originated from four strains: one with the standard arrangement in all chromosomes and the other three with the standard X chromosome arrangement and the same four inversions (about 22% of the genome) in homozygosis in chromosomes II and III. The fitness components are distributed among four fractions of total Darwinian fitness: four of sexual activity, 12 of progeny, nine of time of development and three of duration of emergence period of imagines. Data were analysed for effects of hybridization, variability of expression and relationships between the fitness components, and for heterogeneity of the chromosomal constitutions.

### INTRODUCTION

Adaptation or non adaptation is a qualitative matter. The adaptation degree quantifies the balance between organisms and environment and this can be done by measuring parameters that express the population's ability to survive and reproduce in a certain environment.

According to Yamazaki and Hirose (1984), most of the genes that operate on Darwinian fitness components have different effects on each of them: genes favorable to one component can be deleterious to another, as may occur with pleiotropic effects of mutations on viability (Simmons *et al.*, 1980). Measures of total Darwinian fitness and its components, in *Drosophila*, permit us to infer that genes responsible for fitness are

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not necessarily pleiotropic in the same direction. Therefore, total Darwinian fitness cannot be accurately estimated by one component or just a few measures.

According to Prout (1971a,b), the measure of fitness components in *Drosophila* and other organisms demands extremely laborious experiments, which are commonly carried out under conditions far different from those of the population's natural environment and which are often incomplete because they do not include some potentially important components. One way to avoid spurious estimates of Darwinian fitness is by breaking down selection into partial components embodying, as much as possible, the entire life-cycle.

Hedrick and Murray (1983) considered three basic levels at which intraspecific selection has been studied in *Drosophila*: strains or populations, inversions and individual *loci*. They concluded that the measure of relative fitness of different genotypes is a difficult task and that four different approaches have generally been used. One of them, the most appropriate and convenient, is the sufficient or complete estimation of fitness, which presents the advantage of estimating selection along the whole life-cycle and allows the evaluation of interactions between different fitness components.

Using this approach, Carareto and Mourão (1991a) studied 23 fitness components of *D. prosaltans* covering almost the whole life-cycle. The values obtained were compiled in an adaptation index proposed as a measure of total Darwinian fitness (Carareto and Mourão, 1991b).

In order to identify selective differences among 16 chromosomal constitutions of *D. sturtevanti*, total Darwinian fitness was divided into 28 fitness components which cover almost the whole biological cycle of the species. This paper presents the results concerning the study of these fitness components. The data presented here will be used in a following paper with two purposes: a) to estimate total Darwinian fitness and b) to mathematically establish a hierarchy of the components according to their contribution to total Darwinian fitness.

## MATERIAL AND METHODS

The following four strains of *D. sturtevanti* were used: one with the standard arrangement in all chromosomes (**BRA**) and the other three (**COL**, **COS** and **MEX**) with the standard X chromosome arrangement and the same four inversions in homozygosis in chromosomes II and III. The strain **BRA** was prepared with 18 females collected in 1971 (Mirassol, SP, Brazil), the strain **MEX** was prepared with 40 females and nine males collected in 1973 (Veracruz, VER, Mexico) and the strains **COL** and **COS**, maintained in our laboratory since 1967, were derived from stocks brought from the Genetics Foundation (University of Texas, Austin, USA), respectively labelled as "H 193.3"

(Vilavicencio, Colombia) and "H 158.1" (Turrialba, Costa Rica). A description of the **A**, **B**, **C** and **F** inversions, which comprise about 22% of the genome, is found in Hosaky (1986).

The strains were intra and intercrossed to produce 16 different chromosomal constitutions of three classes: **A**. four structural homozygotes, with chromosomes of the same geographic origin; **B**. six structural heterozygotes; and **C**. six structural homozygotes but heterozygotes for the geographic origin of each set of chromosomes.

Fifty virgin couples of each chromosomal constitution, the sexes aged separately for seven days, were observed for sexual activity during 90 minutes. Groups of 10 couples of each constitution were put into vials and, for each vial, the beginning and the end of each copula were recorded. The couples were then transferred to bottles with fresh corn wheat-arrowroot medium where the progeny was produced.

For each constitution, 10 replicates of mass crosses with 10 couples were made, five of them with the flies used in the sexual activity study. The other five replicates were equally prepared with seven days old flies. For each cross three food vials were used. Dead flies were replaced at each transfer with others taken from reserve bottles prepared exactly as the experimental ones. Thus, the density of 10 couples at the beginning of each half week oviposition period was maintained.

Each bottle (30 for each chromosomal constitution and 480 in all) was observed daily and the day of the appearance of the first pupa was recorded. Flies were counted by sex every half week after imago emergence began; the last counting was done when emergence ceased or at the latest on the 35th day after the date of the cross. After counting, males and females were weighed separately. The pupae were also counted.

The 28 fitness components measured were distributed among four stages of the life-cycle, named as fractions of total Darwinian fitness:

### *A. Sexual Activity*

(1) mating frequency (**MF**); (2) duration of the pre-copula (**DPC**), taken as the time interval between the beginning of the observation of the vial and each copula; (3) absolute duration of the copula (**ADC**), taken as the time interval during which the male remained over the female; (4) relative duration of the copula (**RDC** =  $100 \text{ ADC}/(\text{DPC}+\text{ADC})$ ). Minutes was the time unit for the components of this fraction.

### *B. Progeny*

(5) number of females (**NF**); (6) number of males (**NM**); (7) sex-ratio (**SR** =  $100 \text{ NF}/\text{NM}$ ); (8) total number of imagines (**NI**); (9) absolute (**ANIFC**) and (10) relative (**RNIFC** =  $100 \text{ ANIFC}/\text{NI}$ ) number of imagines in the first counting; (11) daily number

of imagines ( $DNI = NI/DIEP$ ); (12) number of pupae ( $NP$ ); (13) pupa-imago viability ( $PIV = 100 NI/NP$ ); (14) female ( $FIB$ ) and (15) male ( $MIB$ ) individual biomass; (16) sex biomass ratio ( $SBR = 100 FIB/MIB$ ). Milligrams was the unit for biomass.

To estimate time components, the following time intervals were used:  $t$  and  $t'$  for the number of days between the withdrawing of the parental flies from the bottle and the first occurrence of pupae ( $t$ ) or the first counting of imagines ( $t'$ );  $t''$  for the number of days between two successive countings;  $T$  for the number of days in which the parental flies remained in the bottles; and  $T'$  for the number of days between the first and the last countings. After computing the  $EITD$  of the first counting, 3.5 days were added to each of the following countings, producing a grouped data distribution with values  $X_1$  (first counting),  $X_2$  (second counting), and so on, with the frequency of each  $X$  value given by the number of flies in the respective counting.

### C. Time of Development

(17) egg-pupa ( $EPTD = T/2+t$ ), and (18) egg-female ( $EFTD$ ), (19) egg-male ( $EMTD$ ) and (20) egg-imago ( $EITD$ ) time of development ( $= [t'+(t'+t'')]/2+T/2$ ); (21) pupa-imago absolute time of development ( $PIATD=EITD-EPTD$ ); (22) pupa-imago relative time of development ( $PIRTD = 100 PIATD/EITD$ ); absolute time of development in the first counting, (23) of females ( $TDFFC$ ), (24) males ( $TDMFC$ ) and (25) imagines ( $TDIFC$ ) as  $T/2+t'$ .

### D. Duration of Emergence Period

Duration of the emergence period, of (26) females ( $DFEP$ ), (27) males ( $DMEP$ ) and (28) imagines ( $DIEP$ ) as  $T'+(t''/2)$ .

The data were analysed in order to make a comparative study of the 16 chromosomal constitutions, the variability of expression of the 28 fitness components and the pleiotropic effects.

Analyses of variance were performed for homogeneity of means of the 16 constitutions, of the **A**, **B** and **C** classes and of the reciprocal heterozygotes taken together with their parental strains. Differences between means of the same constitution were compared using the Student  $t$  test.

For an evaluation of the heterogeneity of the chromosomal constitutions, each of them was compared to the others, for 27 fitness components (number 1 excluded), by means of multiple comparisons with Scheffé ( $S \alpha = 5.03$ ;  $P = 0.05$ ) and Tukey's tests (see the Appendix for the values).

## RESULTS AND DISCUSSION

Means and standard errors for sexual activity, progeny, time of development and duration of emergence period components are shown in Tables I to V.

The sexual activity study made evident marked differences between the 16 constitutions (Table I), but some of them were associated with specific genetic materials. High mating frequency was associated with chromosomes from Mexico. **MEX** flies presented multiple matings. Hybrids of this strain presented higher mating frequency than those of **BRA**, **COL** and **COS**, although with intermediate values between those of the parental strains.

Multiple matings are common in *Drosophila* (e.g. Richmond and Ehrman, 1974 and Turner and Anderson, 1983), but not in a period shorter than one hour, as was observed in **MEXMEX** flies. Its adaptive significance is not clear. Though concrete data about possible genetic differences related to multiple matings still do not exist, genetic effects are not unexpected. Pyle and Gromko (1981) succeeded in selecting for a decrease in the time between multiple matings of *D. melanogaster* females. Multiple matings in the **MEX** strain, plus an almost uniformly higher mating frequency among its hybrids (compared to other hybrids) suggests a genetically conditioned behavioral difference.

Effects on mating speed are related to chromosomes from Brazil and Colombia. The **COLCOL** constitution and the hybrids with **COL** chromosomes, when of female origin, presented the highest pre-copula times, suggesting an effect of dominance of **COL** chromosomes, of one or both sexes. According to Ehrman and Parsons (1977), faster matings are strongly associated with the male genotype and slower matings with the female one. However, the opposite was also verified: when of female origin the **BRA** chromosomes reduced the duration of pre-copula. Heterokaryotypes for gene arrangements of the same location, often but not always, presented higher mating speed than the homokaryotypes (e.g. Spiess and Langer, 1964a,b; Kaul and Parsons, 1965; Parsons and Kaul, 1966; Spiess *et al.*, 1966 and Spiess and Spiess, 1967). Mating speed of the interpopulational hybrids was evaluated as the mating frequency during the first 15 minutes and the duration of pre-copula. A remarkable decrease of the duration of pre-copula was observed, making evident the high mating speed of some heterozygote chromosomal constitutions (**COLBRA**, **COLCOS**, **COSMEX** and **MEXCOS**).

Costa Rica chromosomes apparently affect the sex-ratio. The sex-ratio distortion observed in the **COS** strain (Table II) was not significantly different from the other three strains; however, the significance in the heterozygotes with **COS** chromosomes suggests the existence of factors disturbing the segregation of the **COS** chromosomes.

A heterotic effect was evident in the productivity of the interpopulational hybrids. All heterozygotes, in both classes, **B** and **C**, yielded a greater number of pupae than the respective homozygotes (Table II), although the differences were not all

significant. According to Dobzhansky and Pavlovsky (1958), in experimental populations with uniform geographic origin, a heterotic effect is maintained, since coadapted gene complexes remain protected from degeneration by the heterozygosis of inversions. In experimental populations with identical gene arrangements, but of different geographical origins, crossing-over produces new combinations that could not exist in nature. Nevertheless, there is evidence that not all recombinants are inferior in fitness (Dobzhansky and Levene, 1951 and Dobzhansky and Pavlovsky, 1953).

Table I - Matings in percentage (in 15 and 90 minutes) and means and standard errors for time of pre-copula and copula of 16 chromosomal constitutions.

Chromosomal constitution	Matings		Pre-copula	Copula	
	90	15		Absolute	Relative
<b>BRABRA</b>	25	13	19.0 ± 3.3	12.5 ± 0.6	49.4 ± 4.7
<b>COLCOL</b>	34	4	37.8 ± 3.2	8.8 ± 0.3	22.9 ± 2.1
<b>COSCOS</b>	37	23	15.6 ± 2.3	10.5 ± 0.7	49.8 ± 4.3
<b>MEXMEX</b>	55	25	24.6 ± 2.9	11.5 ± 0.6	43.6 ± 3.7
<b>F (3,147)</b>			9.53**	5.76**	9.48**
<b>BRACOL</b>	31	6	35.1 ± 4.3	11.4 ± 0.4	33.0 ± 4.0
<b>COLBRA</b>	38	29	11.0 ± 4.3	13.8 ± 0.6	60.6 ± 3.0
<b>F (3,124)</b>			18.39**	18.52**	26.66**
<b>BRACOS</b>	40	13	27.1 ± 3.4	11.3 ± 0.7	38.6 ± 3.7
<b>COBBA</b>	38	25	15.1 ± 2.5	12.5 ± 0.6	54.0 ± 3.6
<b>F (3,136)</b>			3.99**	2.11	2.96*
<b>BRAMEX</b>	39	19	22.4 ± 3.9	16.7 ± 1.0	56.2 ± 4.8
<b>MEXBRA</b>	37	19	19.2 ± 2.8	11.4 ± 0.7	47.5 ± 4.3
<b>F (3,152)</b>			0.68	10.20**	1.66
<b>F (5,217)</b>			6.97**	8.43**	7.06**
<b>COLCOS</b>	40	27	12.2 ± 2.4	13.0 ± 0.6	62.7 ± 4.0
<b>COSCOL</b>	39	13	31.7 ± 4.0	11.7 ± 0.4	36.7 ± 3.3
<b>F (3,146)</b>			15.97**	12.05**	22.49**
<b>COLMEX</b>	47	19	26.0 ± 3.4	12.7 ± 0.7	46.4 ± 4.3
<b>MEXCOL</b>	39	14	30.4 ± 4.0	11.2 ± 0.7	37.1 ± 3.8
<b>F (3,171)</b>			2.48	5.96**	6.85**
<b>COSMEX</b>	45	32	13.2 ± 2.6	12.1 ± 0.4	59.2 ± 3.4
<b>MEXCOS</b>	49	38	11.0 ± 2.1	12.7 ± 0.5	64.6 ± 3.2
<b>F (3,182)</b>			6.14**	2.42	7.20**
<b>F (5,253)</b>			9.48**	1.45	11.47**
<b>F (15,617)</b>			7.68**	6.57**	9.30**

F for homogeneity of means; \* -  $P < 0.05$ ; \*\* -  $P < 0.01$ .

Table II - Means and standard errors for numbers of pupae and imagines, males and females, pupa-imagino viability and sex-ratio.

Chromosomal constitution	Pupae	Imagines	t(58)	Pupa-imagino viability	Females	Males	t(58)	Sex-ratio
<b>BRABRA</b>	272 ± 14	237 ± 13	1.89	88 ± 2	137 ± 5	115 ± 7	2.56*	108 ± 5
<b>COLCOL</b>	316 ± 43	227 ± 28	1.73	78 ± 4	137 ± 15	117 ± 15	1.00	102 ± 5
<b>COSCOS</b>	437 ± 27	308 ± 16	4.09**	75 ± 3	158 ± 9	160 ± 8	0.17	93 ± 3
<b>MEXMEX</b>	395 ± 32	234 ± 20	4.24**	69 ± 5	119 ± 9	123 ± 12	0.28	103 ± 8
<b>F (3,116)</b>	5.73**	3.61*		4.19**	2.67	3.95**		1.22
<b>BRACOL</b>	430 ± 27	334 ± 19	2.90**	81 ± 2	192 ± 6	165 ± 10	2.40**	106 ± 3
<b>COLBRA</b>	452 ± 32	324 ± 18	3.55**	77 ± 3	180 ± 8	159 ± 10	1.64	106 ± 4
<b>F (3,116)</b>	7.97**	7.94**		2.74*	9.71**	6.32**		0.25
<b>BRACOS</b>	477 ± 31	302 ± 15	5.01**	69 ± 4	142 ± 9	165 ± 9	1.77	84 ± 4
<b>COSBRA</b>	580 ± 24	348 ± 18	7.83**	63 ± 4	169 ± 10	177 ± 10	0.55	98 ± 3
<b>F (3,116)</b>	26.43**	8.66**		9.62**	2.86**	10.23**		7.43**
<b>BRAMEX</b>	468 ± 29	267 ± 16	6.13**	64 ± 5	142 ± 8	132 ± 9	0.82	111 ± 6
<b>MEXBRA</b>	479 ± 28	260 ± 21	6.25**	63 ± 6	130 ± 12	127 ± 10	0.85	109 ± 4
<b>F (3,116)</b>	12.65**	0.90		5.93**	1.32	0.53		0.30
<b>F (5,164)</b>	3.29**	4.09**		3.37**	7.17**	4.28**		5.87**
<b>COLCOS</b>	533 ± 38	304 ± 13	5.71**	64 ± 4	146 ± 6	166 ± 8	1.89	88 ± 4
<b>COSCOS</b>	537 ± 44	290 ± 20	5.09**	62 ± 4	142 ± 8	162 ± 12	1.47	84 ± 3
<b>F (3,116)</b>	7.20**	3.57**		4.64**	0.83	4.42**		3.77**
<b>COLMEX</b>	458 ± 43	256 ± 20	4.22**	66 ± 5	140 ± 9	132 ± 12	0.51	101 ± 6
<b>MEXCOL</b>	501 ± 45	287 ± 19	4.38**	69 ± 5	150 ± 9	153 ± 11	0.19	90 ± 3
<b>F (3,116)</b>	3.77**	1.52		1.34	1.57	1.71		1.14
<b>COSMEX</b>	563 ± 33	248 ± 19	7.29**	53 ± 6	98 ± 9	139 ± 10	3.09**	80 ± 3
<b>MEXCOS</b>	540 ± 34	265 ± 11	7.79**	56 ± 5	101 ± 4	152 ± 7	6.07**	78 ± 5
<b>F (3,116)</b>	6.46**	3.90*		4.63**	12.27**	3.14*		5.35**
<b>F (5,174)</b>	0.87	1.68		1.66	9.40**	1.71		4.22**
<b>F (15,464)</b>	6.20**	4.21**		4.63**	7.96**	3.90**		5.97**

F for homogeneity of means; t for differences between means; \* = P < 0.05; \*\* = P < 0.01.

Differential survival of individuals carrying different gene arrangements depends on food and vital space. Ability to survive and reproduce in crowded conditions should represent one major adaptive character. Birch (1955) showed that the **CH** arrangement of *D. pseudoobscura* is fitter than **ST** in crowded environments, the opposite occurring at low density.

The data obtained allowed analysis of some questions concerning coadaptation and effects of high larval density on fitness components. *D. sturtevantii* has a peculiar characteristic: experimental and stock bottles always present a dense layer of pupae submerged in the culture medium, from which no imagines emerge (Machado, 1976). For this reason the pupa-imago viability was measured.

The heterozygote constitutions, in spite of being more productive in terms of number of pupae, presented pupa-imago viability lower than the parental homozygotes. This fact and the very few larvae found when the pupae were counted indicate that in *D. sturtevantii*, under crowded conditions, as was the case in the experimental bottles, hard selection occurs at the pupal stage. This conclusion agrees with the works of Park (1938) in *Tribolium*, and Sang (1949) and Moya and Botella (1985), in *Drosophila*, who showed that pupal mortality is a density dependent process. The effect of density causing delay of development (e.g. Ohba, 1961 and Bakker and Podger, 1970), studied for *Drosophila* gene arrangements, has shown that heterozygotes for arrangements of the same locality grow faster than the homozygotes (Dobzhansky and Spassky, 1944; Brncic *et al.*, 1969 and Budnik *et al.*, 1971).

Time of development and duration of imagines emergence period of **B** and **C** classe heterozygotes (Tables IV and V) were longer than those of the homozygotes, which is a possible negative effect of density. This result contributes to our understanding of heterotic effects on productivity. In spite of the different geographical origins, without any possibility of coadaptation, the gene arrangements interact, favorably or not, depending on the genetic background.

The interaction between the gene arrangements in the heterozygotes of the **B** class, protected from recombination by structural heterozygosis, as well as in those of the **C** class, had a positive effect on pupa production. Nevertheless, for this stage, under hard density dependent selection the imbalance between the greater part of the non-coadapted gene complexes was disclosed by viability and rate of development reduction and by a longer duration of the imaginal emergence period.

Interaction effects were positive and effective on **BRA** vs **COL** chromosomal materials, overcoming the effects of density dependent hard selection and leading to a greater production of imagines by **BRACOL** and **COLBRA** hybrids (Table II). When considered solely with regard to the number of pupae for **BRA** vs **COL** heterozygotes, this seems to corroborate Singh's (1985) proposition that coadaptation should not be geographically circumscribed and that heterozygosis to genes and gene complexes can

Table III - Means and standard errors for number of imagines, daily and in the first counting, female and male individual biomass and sex biomass ratio.

Chromosomal constitution	Number			Biomass (mg)			Ratio
	Absolute	Relative	Daily	Females	Males	t(58)	
<b>BRABRA</b>	12.0 ± 4.6	4.6 ± 1.4	31.0 ± 1.6	1.31 ± 0.02	0.93 ± 0.01	2.56*	70.8 ± 0.6
<b>COLCOL</b>	63.9 ± 9.8	36.2 ± 5.1	26.0 ± 4.7	1.34 ± 0.04	1.03 ± 0.03	5.59**	77.6 ± 1.4
<b>COSCOS</b>	33.3 ± 4.6	11.9 ± 1.8	26.6 ± 1.4	1.26 ± 0.02	1.01 ± 0.02	8.27**	80.6 ± 0.8
<b>MEXMEX</b>	24.7 ± 5.9	14.7 ± 4.0	18.1 ± 1.9	1.34 ± 0.03	1.08 ± 0.02	7.29**	80.5 ± 1.0
<b>F (3,116)</b>	11.32**	15.76**	8.82**	1.44	8.06**		21.63**
<b>BRACOL</b>	27.0 ± 4.2	8.3 ± 1.2	30.6 ± 1.8	1.24 ± 0.04	0.88 ± 0.02	8.56**	72.2 ± 1.1
<b>COLBRA</b>	32.0 ± 7.8	10.2 ± 2.0	26.7 ± 1.7	1.25 ± 0.02	0.89 ± 0.02	13.51**	71.7 ± 0.6
<b>F (3,116)</b>	9.76**	24.94**	1.97	2.29	10.60**		9.52**
<b>BRACOS</b>	30.6 ± 6.2	11.0 ± 2.4	24.5 ± 1.4	1.24 ± 0.02	0.99 ± 0.02	7.21**	80.0 ± 1.1
<b>COSBRA</b>	10.9 ± 2.2	3.1 ± 0.6	23.9 ± 1.4	1.26 ± 0.01	0.96 ± 0.01	16.61**	76.1 ± 0.8
<b>F (3,116)</b>	6.56**	6.91**	4.95**	1.80	5.09**		28.09**
<b>BRAMEX</b>	12.0 ± 2.1	5.5 ± 1.2	19.4 ± 1.6	1.30 ± 0.02	0.98 ± 0.02	10.65**	75.6 ± 0.8
<b>MEXBRA</b>	12.4 ± 3.6	5.4 ± 1.5	21.4 ± 2.4	1.32 ± 0.02	0.97 ± 0.02	14.12**	75.2 ± 1.0
<b>F (3,116)</b>	2.11	4.24**	9.54**	0.56	12.35**		20.48**
<b>F (5,174)</b>	4.36**	3.68**	5.16**	2.09	7.05**		10.25**
<b>COLCOS</b>	30.7 ± 4.6	10.5 ± 1.5	25.2 ± 1.6	1.25 ± 0.02	0.97 ± 0.01	10.85**	77.6 ± 0.7
<b>COSCOL</b>	24.0 ± 3.0	10.8 ± 1.9	23.8 ± 1.7	1.26 ± 0.04	0.99 ± 0.02	6.01**	79.4 ± 0.6
<b>F (3,116)</b>	8.47**	18.06**	0.50	1.52	1.55		2.18
<b>COLMEX</b>	41.6 ± 6.7	19.3 ± 3.1	20.0 ± 1.6	1.35 ± 0.03	1.04 ± 0.02	8.82**	77.0 ± 0.8
<b>MEXCOL</b>	30.6 ± 7.0	13.4 ± 3.2	20.7 ± 1.4	1.29 ± 0.03	1.00 ± 0.02	7.79**	78.3 ± 1.0
<b>F (3,116)</b>	5.13**	7.17**	3.45**	0.73	1.61		2.02
<b>COSMEX</b>	6.8 ± 1.8	2.8 ± 0.7	18.3 ± 1.9	1.33 ± 0.02	1.06 ± 0.02	11.59**	79.3 ± 0.6
<b>MEXCOS</b>	10.4 ± 1.9	4.0 ± 0.7	18.6 ± 1.5	1.40 ± 0.02	1.11 ± 0.01	13.17**	79.4 ± 1.1
<b>F (3,116)</b>	9.67**	6.82**	6.12**	6.52**	5.54**		0.55
<b>F (5,174)</b>	8.09**	8.49**	3.00*	4.87**	8.19**		1.40
<b>F (15,464)</b>	7.81**	12.14**	5.85**	3.22**	10.57**		11.56**

F for homogeneity of means; t for differences between means; \* = P < 0.05; \*\* = P < 0.01.

Table IV - Means and standard errors for time of development fitness components.

Chromosome constitution	Egg-pupa		Pupa-imag		t(58)	Pupa-imag		t(58)	Egg-female		Egg-male	t(58)	Egg-imag
	Absolute	Absolute	Absolute	Relative		Relative	Relative		Relative				
<b>BRABRA</b>	11.2 ± 0.2	8.5 ± 0.2	9.50**	43 ± 1.0	18.9 ± 0.2	20.3 ± 0.2	5.21**	19.6 ± 0.2					
<b>COLCOL</b>	8.4 ± 0.2	9.3 ± 0.3	2.57*	52 ± 1.1	17.0 ± 0.3	18.4 ± 0.3	2.90**	17.7 ± 0.3					
<b>COSCOS</b>	9.4 ± 0.1	10.6 ± 0.3	3.41**	53 ± 0.9	19.2 ± 0.3	20.8 ± 0.3	3.56**	20.0 ± 0.3					
<b>MEXMEX</b>	9.4 ± 0.1	13.8 ± 0.9	4.88**	58 ± 1.8	22.0 ± 0.8	24.1 ± 0.9	1.57	23.1 ± 0.9					
<b>F (3,116)</b>	62.99**	20.15**		23.56**	19.01**	8.06**		20.27**					
<b>BRACOL</b>	9.3 ± 0.1	10.9 ± 0.3	4.20**	54 ± 1.1	19.5 ± 0.3	21.0 ± 0.3	3.86**	20.2 ± 0.3					
<b>COLBRA</b>	9.5 ± 0.1	11.2 ± 0.4	4.33**	54 ± 0.9	20.3 ± 0.4	21.1 ± 0.3	1.53	20.7 ± 0.4					
<b>F (3,116)</b>	58.99**	16.21**		25.38**	21.69**	16.98**		19.82**					
<b>BRACOS</b>	8.8 ± 0.2	12.7 ± 0.6	6.65**	58 ± 1.1	20.3 ± 0.5	22.4 ± 0.5	2.72**	21.5 ± 0.5					
<b>COSBRA</b>	9.7 ± 0.1	13.6 ± 0.3	11.61**	58 ± 0.6	23.0 ± 0.4	23.7 ± 0.3	1.72	23.3 ± 0.3					
<b>F (3,116)</b>	53.22**	36.35**		60.22**	24.69**	20.15**		21.59**					
<b>BRAMEX</b>	9.2 ± 0.1	14.4 ± 0.6	7.91**	60 ± 1.3	22.4 ± 0.6	25.0 ± 0.7	2.91**	23.7 ± 0.6					
<b>MEXBRA</b>	9.6 ± 0.1	13.8 ± 0.6	6.63**	58 ± 1.2	22.9 ± 0.6	23.8 ± 0.6	2.70**	23.4 ± 0.6					
<b>F (3,116)</b>	37.60**	18.99**		33.76**	9.19**	9.76**		9.30**					
<b>F (5,174)</b>	7.23**	8.42**		6.25**	10.47**	11.05**		10.03**					
<b>COLCOS</b>	8.9 ± 0.1	12.5 ± 0.6	6.37**	56 ± 1.3	20.6 ± 0.5	22.0 ± 0.5	1.90	21.4 ± 0.5					
<b>COSCOL</b>	9.0 ± 0.1	12.1 ± 0.5	5.64**	56 ± 1.4	20.2 ± 0.5	21.9 ± 0.4	2.70**	21.1 ± 0.4					
<b>F (3,116)</b>	10.04**	10.40**		5.71**	14.28**	18.08**		16.77**					
<b>COLMEX</b>	9.0 ± 0.2	12.3 ± 0.7	4.77**	58 ± 1.4	20.5 ± 0.7	21.9 ± 0.7	1.49	21.3 ± 0.7					
<b>MEXCOL</b>	9.0 ± 0.1	13.4 ± 0.7	5.90**	58 ± 1.5	21.3 ± 0.7	23.3 ± 0.7	2.11*	22.4 ± 0.7					
<b>F (3,116)</b>	8.54**	8.48**		3.80**	11.69**	13.30**		12.59**					
<b>COSMEX</b>	9.5 ± 0.1	15.4 ± 0.6	8.93**	61 ± 1.3	24.1 ± 0.6	25.5 ± 0.6	1.65	24.9 ± 0.6					
<b>MEXCOS</b>	9.1 ± 0.2	15.4 ± 0.6	10.13**	61 ± 1.2	23.1 ± 0.6	25.6 ± 0.6	2.94**	24.6 ± 0.6					
<b>F (3,116)</b>	1.22	12.16**		10.18**	12.07**	12.66**		12.73**					
<b>F (5,174)</b>	2.09	5.99**		3.20**	7.12**	9.09**		8.09**					
<b>F (15,464)</b>	19.24**	13.14**		13.90**	12.68**	14.29**		13.49**					

F for homogeneity of means; t for differences between means; \* = P &lt; 0.05; \*\* = P &lt; 0.01.

Table V - Means and standard errors for time fo development at the first counting and duration of the emergence period.

Chromosomal constitution	Time of development in the first counting				Duration of the emergence period			
	Females	Males	t(58)	Imagines	Females	Males	t(58)	Imagines
<b>BRABRA</b>	15.4 ± 0.3	16.6 ± 0.3	2.72**	15.4 ± 0.3	7.5 ± 0.4	6.8 ± 0.3	1.31	7.9 ± 0.4
<b>COLCOL</b>	14.1 ± 0.3	14.4 ± 0.2	0.71	14.4 ± 0.3	7.6 ± 0.7	8.1 ± 0.8	0.46	8.9 ± 0.8
<b>COSCOS</b>	14.0 ± 0.0	15.0 ± 0.3	3.51**	14.0 ± 0.0	11.0 ± 0.5	10.9 ± 0.7	0.20	12.0 ± 0.6
<b>MEXMEX</b>	14.6 ± 0.2	15.6 ± 0.4	2.24*	14.6 ± 0.2	14.0 ± 1.0	14.0 ± 0.9		14.5 ± 1.0
<b>F (3,116)</b>	7.98**	8.83**		6.23**	19.52**	19.27**		17.76**
<b>BRACOL</b>	14.0 ± 0.2	15.2 ± 0.3	3.34**	14.0 ± 0.2	10.7 ± 0.7	10.7 ± 0.7		11.4 ± 0.7
<b>COLBRA</b>	14.4 ± 0.2	14.4 ± 0.2		14.4 ± 0.2	11.7 ± 0.7	12.8 ± 0.8	1.00	12.9 ± 0.7
<b>F (3,116)</b>	7.80**	15.58**		6.29**	11.35**	16.54**		11.65**
<b>BRACOS</b>	14.6 ± 0.2	14.9 ± 0.3	0.93	14.6 ± 0.2	12.4 ± 0.8	12.9 ± 0.8	0.42	13.2 ± 0.8
<b>COSBRA</b>	14.9 ± 0.3	15.6 ± 0.3	1.62	15.3 ± 0.3	14.6 ± 0.6	14.3 ± 0.6	0.40	15.0 ± 0.6
<b>F (3,116)</b>	5.71**	6.20**		6.58**	24.92**	26.02**		26.49**
<b>BRAMEX</b>	15.0 ± 0.3	16.1 ± 0.4	2.47*	15.0 ± 0.3	14.3 ± 0.8	14.9 ± 1.0	0.44	15.6 ± 0.9
<b>MEXBRA</b>	15.6 ± 0.4	16.2 ± 0.4	1.09	15.5 ± 0.4	14.2 ± 1.0	14.1 ± 1.0	0.09	14.5 ± 0.9
<b>F (3,116)</b>	2.27	1.11		1.91	15.38**	19.36**		17.69**
<b>F (5,174)</b>	4.49**	5.20**		4.49**	4.40**	3.47**		4.04**
<b>COLCOS</b>	14.0 ± 0.0	14.6 ± 0.2	2.39*	14.6 ± 0.2	12.0 ± 0.8	12.4 ± 0.8	0.44	13.0 ± 0.7
<b>COSCOL</b>	14.1 ± 0.1	14.7 ± 0.3	2.05*	14.1 ± 0.2	11.7 ± 0.7	12.4 ± 0.8	0.67	12.7 ± 0.6
<b>F (3,116)</b>	0.31	1.21		1.92	9.17**	7.28**		6.71**
<b>COLMEX</b>	14.4 ± 0.2	14.5 ± 0.2	0.69	14.5 ± 0.2	12.8 ± 1.0	13.5 ± 1.0	0.51	13.7 ± 0.9
<b>MEXCOL</b>	14.9 ± 0.3	15.8 ± 0.4	1.76	14.9 ± 0.3	13.4 ± 0.8	14.1 ± 0.9	0.53	14.6 ± 0.8
<b>F (3,116)</b>	2.20	5.40**		0.99	9.91**	10.35**		9.36**
<b>COSMEX</b>	15.4 ± 0.3	16.8 ± 0.4	2.95**	15.4 ± 0.3	15.4 ± 0.8	14.5 ± 0.8	0.71	15.6 ± 0.8
<b>MEXCOS</b>	14.8 ± 0.3	16.3 ± 0.4	3.01**	14.8 ± 0.3	15.7 ± 0.8	14.9 ± 0.9	0.70	15.9 ± 0.8
<b>F (3,116)</b>	5.67**	4.30**		5.67**	7.00**	4.82**		5.33**
<b>F (5,174)</b>	5.59**	9.76**		3.04**	4.07**	1.51		2.79**
<b>F (15,464)</b>	4.97**	6.76**		3.84**	9.55**	8.66**		8.90**

F for homogeneity of means; t for differences between means; \* = P < 0.05; \*\* = P < 0.01.

produce high fitness without previous coadaptation. Two fitness components which seem to have a similar genetic basis, time of development and viability (*cf.* Yoshimaru and Mukai, 1985), give evidence of the lack of coadaptation in the **BRA** vs **COS** and **BRA** vs **MEX** heterozygotes.

Heterozygosis for the same inversions from different localities (**COL**, **COS** e **MEX**) made it possible to break down the supergenes through recombination. However, negative effects of recombination were expressed solely in the developmental stage by density dependent hard selection.

Results concerning the heterogeneity of the chromosomal constitutions are shown in Figure 1 where each bar represents the number of differences computed as a percentage of 405 comparisons (15 times 27). The **MEXCOL** constitution presented the smallest and **MEXCOS** the largest values. The chromosomal constitutions were separated into three groups according to the frequency of significant differences: with low frequency (up to 12%) are **BRACOS**, **COLCOS** and **MEXCOL**; with an intermediate one (between 12% and 24%), **COSCOS**, **MEXMEX**, **BRACOL** and **COLBRA**, **COSBRA**, **BRAMEX** and **MEXBRA**, **COSCOL** and **COLMEX**; and with high frequency (above 24%), **BRABRA**, **COLCOL**, **COSMEX** and **MEXCOS**.

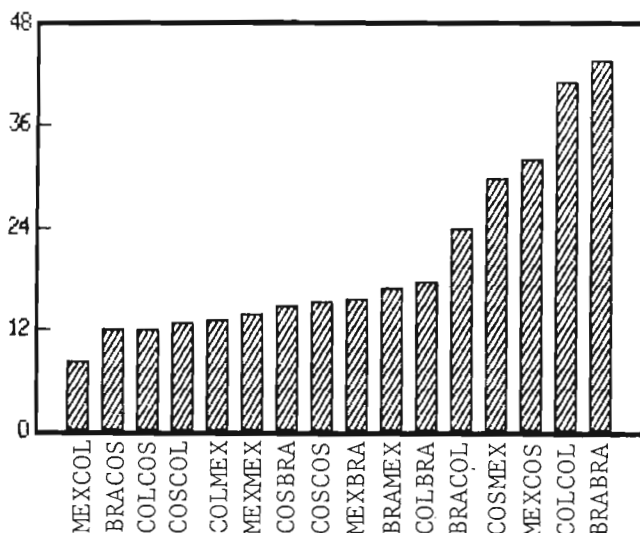


Figure 1 - Frequencies (in percentage on the ordinate) of significant differences between each chromosomal constitution and the 15 others, for 27 fitness components (abscissa).

Based on the assumption that fitness components are positively correlated with total Darwinian fitness, in most of the studies only one or a few fitness components are measured. However, there is experimental evidence of positive, negative or absence of correlation between components as well as between components and total Darwinian fitness (e.g. Hiraizumi, 1961; Mourão *et al.*, 1972; Yamazaki and Hirose, 1984 and Carareto and Mourão, 1991a).

Rose (1983) examined several hypotheses about evolution of life-history traits, including the unitary, the particulated and the pleiotropic hypotheses. This last, being antagonistic or variable, is based on negative correlations between gene effects on different life-history traits and thus it can be generalized to a variety of patterns of life-history evolution.

Fitness components associations were analyzed through simple correlation coefficients between means of the 16 chromosomal constitutions for 62 pairs of components, either from the same or from different fractions. The significant *r* values (14 DF) are presented in Table VI. Out of the 62 simple correlation analyses, the 23 highly significant (*r* values between 0.698 and 0.970), showed two groups of pleiotropic effects

Table VI - Correlation coefficients between means of the 16 chromosomal constitutions.

Components	<i>r</i>	t(14)	Components	<i>r</i>	t(14)
NF vs NM	0.509	2.21*	EPATD vs ATDIFC	-0.509	2.21*
vs FIB	-0.744	4.58**	PIATD vs EIATD	0.957	12.67**
vs PIATD	-0.505	2.19*	vs DIEP	0.964	13.58**
vs EIATD	-0.512	2.23*	EFATD vs EMATD	0.962	13.18**
FIB vs MIB	0.755	4.31**	vs ATDFFC	0.616	2.93*
NP vs DNI	-0.499	2.15*	vs DFEP	0.942	10.47**
vs PIV	-0.851	6.08**	EMATD vs ATDMFC	0.645	3.16*
vs PIATD	0.768	4.49**	vs DMEP	0.867	6.52**
vs EIATD	0.698	3.65**	EIATD vs PIRTD	0.794	4.90**
vs DIEP	0.806	5.09**	vs ATDIFC	0.560	2.53*
ANIFC vs ATDIFC	-0.501	2.17*	vs DIEP	0.913	8.38**
DNI vs PIATD	-0.863	6.39**	PIRTD vs DIEP	0.919	8.75**
vs EIATD	-0.784	4.70**	vs DNI	-0.801	5.00**
PIV vs DNI	0.815	5.26**	ATDFFC vs ATDMFC	0.853	6.14**
vs PIATD	-0.913	8.38**	DFEP vs DMEP	0.969	14.68**
vs EIATD	-0.838	5.74**			
vs PIRTD	-0.893	7.44**			

t for significance of *r*; \* -  $P < 0.05$ ; \*\* -  $P < 0.01$ .

(Table VI): eight negative in the first group (NF vs FIB, NP vs PIV, DNI vs PIATD, DNI vs EITD, PIV vs PIATD, PIV vs EITD, PIV vs PIRTD, PIRTD vs DNI) and 15 positive in the second (FIB vs MIB, NP vs PIATD, NP vs EITD, NP vs DIEP, PIV vs DNI, PIATD vs EITD, PIATD vs DIEP, EFTD vs EMTD, EFTD vs DFEP, EMTD vs DMEP, EITD vs PIRTD, EITD vs DIEP, PIRTD vs DIEP, TDFFC vs TDMFC and DFEP vs DMEP). There is a third group with correlations varying from weak (0.560 and 0.616: EMTD vs TDMFC and EFTD vs TDFFC) to  $r$  values very close to the significant level value (between 0.499 and 0.560), these being five negative (NF vs PIATD, NF vs EITD, NP vs DNI, ANIFC vs TDIFC and EPTD vs TDIFC) and two positive (NF vs NM and EITD vs TDIFC). The remaining 30 non-significant correlations correspond to an absence of pleiotropic effects. These results are in agreement with the antagonistic or variable pleiotropism hypothesis, which shows, also in *D. sturtevantii*, that genes or gene complexes are not necessarily pleiotropic in the same direction.

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### RESUMO

Este é um estudo de 28 componentes do valor adaptativo de 16 constituições cromossômicas de *Drosophila sturtevantii* originadas de quatro linhagens: uma com o arranjo padrão em todos os braços cromossômicos e as outras três com o arranjo padrão no cromossomo X e as mesmas quatro inversões em homozigose nos demais cromossomos, correspondendo a 22% do genoma. Os componentes estão distribuídos em quatro frações do valor adaptativo total: quatro da atividade sexual, 12 da progênie, nove do tempo de desenvolvimento e três da duração do período de emergência dos imagos. Os dados foram analisados para verificar efeitos da hibridação, a variabilidade de expressão e interações entre os componentes, e a heterogeneidade das constituições.

### APPENDIX

Tukey values ( $P = 0.05$ ) for multiple comparison of means.

NF	43	PIV	21	PIATD	2.7
NM	49	FIB	0.13	PIRTD	6
SR	22	MIB	0.09	TDFFC	1.2
NI	87	SBR	4	TDMFC	1.5
ANIFC	25.5	EPTD	0.7	TDIFC	1.2
RNIFC	11.4	EFTD	2.6	DFEP	3.8
DNI	8.3	EMTD	2.6	DMEP	5.8
NP	164	EITD	2.6	DIEP	3.8

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