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DARWINIAN FITNESS IN *Drosophila*. II. QUANTIFICATION OF TOTAL FITNESS IN *Drosophila prosaltans**

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ABSTRACT

An evaluation was made of Darwinian fitness and the relative importance, for total fitness, of 23 fitness components, covering almost the entire lifespan of *Drosophila prosaltans* females. Three strains, from Brazil, Costa Rica and Trinidad Tobago were used. Total fitness was divided into four fractions (sexual activity, inseminated and uninseminated females activity and progeny) which were combined into two indices, *W'* and *W''*, proposed as representative of total Darwinian fitness. The inseminated female and progeny fraction values, involving almost all the components related to productivity and viability, gave the highest *W'* and *W''* values for the Brazil strain when compared to the others. A striking heterogeneity of the strains was disclosed by an analysis of the hierarchical order of the relative importance of the components, which implies different adaptive strategies. Mating frequency, duration of the pre-copula, time to first copula, longevity, number of eggs (total and daily), pupae and imagines, and duration of pupation and of imaginal emergence period had different degrees of importance in each strain, suggesting a prominent role of these components for the total fitness. The methods employed to study the complex problem of estimating Darwinian fitness (*W'* and *W''*) and for the relative importance of its fractions or components were shown to be proper and sensible for these purposes and for detecting intra and interstrain variability.

INTRODUCTION

Evolution is nothing more than what Charles Darwin called "descent with modification". Natural selection does not act at random on the gene pool of the popula-

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tions, so there is a differential perpetuation of genetic variants. Thus, the best adjusted genotypes will yield more descendents and consequently their frequencies will progressively increase.

The corollary of natural selection is Darwinian fitness which is, for the individual, simply the number of fertile descendents in the next generation (Knight and Robertson, 1957) and, for the genotype, the descent expectation (Fisher, 1930). According to Mettler and Gregg (1969), there are several models to estimate fitness. Most of the present knowledge is derived from simple models based upon allelic frequencies of one *locus*. When one gene is subject to selection pressure its frequency in the offspring is not the same as that in the parents, since parents of different genotypes unequally pass on their genes to the next generation (Falconer, 1981). Natural selection changes gene and genotype frequencies, by changing viability or fecundity, or both.

According to Christiansen (1984), natural selection may act at any stage in the life cycle of an organism and the object of selection may differ over the stages; in a diploid sexually reproducing organism selection may act on gametes, individuals or combinations of individuals, in each case with different evolutionary consequences. Prout (1971a,b) pointed out that spurious estimates of fitness can be avoided when total fitness is broken down into partial components. Clark *et al.* (1981) recommended that experimental fitness estimates should be fractionized into components such as viability and sexual or gametic selection. Hiraizumi (1961) showed that total fitness is a result of several components and even the most trivial ones can contribute to fitness through one or more of the many biochemical development paths. For the latter author, the interrelation between biochemical paths is very intricate, however the traits can be grouped into classes even if the relationships between the components of each class are not understood.

According to Mackay (1985) natural selection acts on Darwinian fitness in such a way that several fitness components are simultaneously selected, with different effects on each of them. Prediction of responses to natural selection requires the identification of all the characters which together comprise fitness, their relative weights, their phenotypic and genetic variances and covariances with fitness and with each other. The construction of an index would enable one to predict not only the responses of the population to natural selection in different habitats, in which the relative weights of the components may vary, but also the evolution of the component characters as a correlated response.

Although the core of the Darwinian fitness concept is a clearly understood matter, measuring it is a permanent challenge for population genetics. Therefore, not many estimates of total fitness are known for *Drosophila* species (*e.g.* Sved and Ayala, 1970; Sved, 1971; Mourão *et al.*, 1972; Tracey and Ayala, 1974; Sved, 1975; Wilton and Sved, 1979; Polivanov, 1981; Clarck *et al.*, 1981 and Seager *et al.*, 1982).

Evaluation of the degree of importance of fitness components for total fitness practically does not exist. Probably the only attempt is that of Wills (1981), using 289 heritability estimates concerning more than 20 fitness components of domestic fowl, cattle and swine; he listed the fitness components in what seemed to him to be the descending order of importance for total fitness.

The experimental procedures employed made it possible to measure 23 fitness components covering practically the whole lifespan of *D. prosaltans* females. The way the data were analysed binds together the components in the total fitness indices using a multiplicative effect model and makes possible to quantify the importance of each component for total Darwinian fitness.

MATERIALS AND METHODS

Two adaptation indices, W' and W'', are proposed as measures of total Darwinian fitness. The experiments carried out with three strains of *D. prosaltans*, from Brazil (*BR*), Costa Rica (*CR*) and Trinidad Tobago (*TR*) are described elsewhere (see Carareto and Mourão, 1991, this issue). The data used in the calculation of the W' and W'' values are found in the above mentioned paper (see Tables I to VI and text for mating frequency).

Total fitness was divided into four fractions: SA', standing for the sexual activity fraction, includes mating frequency (*MF*), duration of the pre-copula (*DPC*), time to first copula in each mating box (*TFC*), and absolute (*ADC*) and relative (*RDC*) duration of the copula; UI' and I', standing respectively for the inseminated and uninseminated female activity fractions, includes longevity (*L*), absolute (*AOP*) and relative (*ROP*) duration of the oviposition period, and total (*TNE*) and daily (*DNE*) number of eggs; and P', standing for the progeny fraction, includes number of viable eggs (*NVE*), pupae (*NP*) and imagines (*NI*), egg-pupa (*EPV*), pupa-imago (*PIV*) and egg-imago (*EIV*) viability, and duration of pupation (*DPP*) and imaginal emergence period (*DIEP*). So that:

$$SA' = (MF)\,(1/DPC)\,(1/TFC)\,(1/ADC)\,(RDC),$$

$$UI' = I' = (L)\,(AOP)\,(ROP)\,(TNE)\,(DNE) \text{ and}$$

$$P' = (NVE)\,(NP)\,(NI)\,(EPV)\,(PIV)\,(EIV)\,(DPP)\,(DIEP),$$

$$W' = (SA')\,(UI')\,(I')\,(P')$$

Each of the above terms is a mean of percentages, taking each female measure as a percentage of the average of the three strains means for the UI' and I' fitness components. For the components of SA' (*MF* excluded) and P' the measures were calculated as percentage of the weighted average of the three strains means. The *MF* component of each strain was calculated as a percentage of the mating frequency average of the three strains.

In the adaptation index $W'' = (SA'')(UI'')(I'')(P'')$, the term SA'' is an average of the four percentages of each mated female of each strain. The terms UI'', I'' and P'' are respectively means of n UI, n I and n P values, n standing for the number of uninseminated and inseminated females of each strain. A UI value was computed for each female as the average of the five percentages of the uninseminated females fraction, the same procedure being used in computing the I and P values. The percentages here are the same used in the calculation of SA', UI', I' and P'. Before computing W' and W'' of each strain, the respective percentage values of SA', UI', I', P', UI'', I'' and P'' were transformed into decimals.

The formulae for W' and W'' were based on the following assumptions: (1) high mating frequency and high relative duration of copula are better than low ones, since a larger number of females can yield progeny and more time is available for male gamete transfer; for the other three sexual activity components lower values mean more efficiency, that is, a faster mating; (2) as for the *UI* and *I* components, higher values mean more efficiency, since the females remain longer in the environment, may lay more eggs and consequently have a larger progeny; and (3) higher values of all the *P* components are obviously better than lower ones because they correspond to more descendents. According to the assumptions above, the *DPC, TFC* and *ADC* components percentage values were inverted.

In short, while W' is computed with basis on fitness component means of the females sampled in each strain, W'' is computed based on total fitness values obtained for each female of each strain.

The 23 components were evaluated for their relative contribution to the total fitness of each strain. This was done, for each strain, first summing the 23 percentual means taken as defined in the above assumptions, and then computing every mean as a percentage of the respective sum. For each strain, the relative contribution of each fraction was obtained in a similar way: first summing the percentage means of the fraction and then computing each of these means as a percentage of the sum of the four mean values.

RESULTS

Tables I to III present the percentual means used to compute the W' values for Table IV.

Three of the sexual activity components, duration of the pre-copula, absolute duration of the copula and time to first copula (Table I), of the *CR* strain had the highest percentual values, however the analysis of variance *F* value was significant only for the last of these. The *CR* strain had the highest SA' score (Table IV), about three times larger than for *BR*.

Table I - Means and standard errors of percentages of the sexual activity fraction components of the *BR*, *CR* and *TR* strains.

Component	*BR* (20)	*CR* (32)	*TR* (38)	*F*
Mating frequency	66.7	106.7	126.7	
Duration of pre-copula	123.0 ± 13.7	151.0 ± 19.0	126.0 ± 10.0	1.05
Duration of copula				
Absolute	111.4 ± 4.3	131.0 ± 12.4	107.2 ± 10.6	1.43
Relative	95.4 ± 5.0	97.7 ± 6.5	104.4 ± 6.7	0.51
Time to 1st copula	84.5 ± 12.7	146.7 ± 23.4	114.1 ± 7.1	3.75*

Mating frequency in percentage.
F for homogeneity of means; *: $P < 0.05$.
Number of females in parentheses.

Contrary to the sexual activity fraction, the three *UI'* scores were nearly equal (Table IV), but due to different causes. The *BR* strain had the highest number of eggs and *TR* flies were the most long-lived, with the longest duration of the oviposition period (Table II). On the other hand, the *I'* score of the *TR* strain is only about half of that of the other two strains (Table IV).

For the *P'* scores striking differences can be noticed (Table IV): the *BR* score is respectively 65 and 11 times higher than the *CR* and *TR* ones. In fact, as it can be seen in Table III, the highest number of eggs, pupae and imagines and the greatest of two viabilities (egg-pupa and egg-imago) were those of *BR*, while *TR* had the highest values of the other three components (pupa-imago viability and duration of pupation and imaginal emergence period). The *BR* adaptation index value *W'* was about 23 and eight times higher than the *CR* and *TR* values, respectively.

Figures 1 and 2 show graphically the relative contribution respectively of the four fractions and the 23 fitness components for the total fitness expressed by the *W'* scores of Table IV. The total fitness of the *BR* strain is due mostly to the *I* and *P* components, and that of the *CR* strain to the *SA* and *I* ones. For the *TR* strain *SA* is the most important fraction (Figure 1).

Table II - Means and standard errors of percentages of the uninseminated (*UI*) and inseminated (*I*) females activity fraction components of the *BR*, *CR* and *TR* strains.

Component		*BR*	*CR*	*TR*	*F*
Longevity	*UI*	74.7 ± 7.0	104.7 ± 7.7	111.2 ± 14.1	5.31**
	I	97.1 ± 6.6	110.7 ± 6.7	107.6 ± 7.8	0.68
Oviposition					
Absolute	*UI*	77.1 ± 10.0	82.5 ± 14.1	115.6 ± 22.5	1.73
	I	94.9 ± 7.7	101.9 ± 10.0	123.8 ± 12.1	1.84
Relative	*UI*	91.9 ± 9.0	76.9 ± 11.7	99.4 ± 13.0	0.91
	I	106.5 ± 4.4	97.4 ± 5.9	118.3 ± 3.8	5.41**
Number of eggs					
Total	*UI*	99.3 ± 16.7	82.9 ± 17.1	76.2 ± 16.2	0.46
	I	142.5 ± 9.6	119.6 ± 10.4	80.2 ± 5.9	13.35**
Daily	*UI*	95.2 ± 9.3	69.3 ± 10.8	59.8 ± 9.0	3.27**
	I	149.7 ± 18.4	143.0 ± 23.0	72.6 ± 6.5	7.46**

F for homogeneity of means; **: $P < 0.01$.

UI and *I* respectively for uninseminated and inseminated females.

Number of females: for *BR* 31 *UI* and 19 *I*;
for *CR* 20 *UI* and 30 *I*;
for *TR* 13 *UI* and 37 *I*.

In Figure 2 the *BR* percentual means are in increasing order of the respective values. For the other two strains the same order of the fitness components was maintained. In this way the differences between the strains become evident. Three criteria were used to distinguish the main features of the relative importance of the 23 fitness components for the total fitness of the strains studied.

Table III - Means and standard errors of percentages of the progeny fraction components of the *BR*, *CR* and *TR* strains.

Component	*BR* (19)	*CR* (30)	*TR* (37)	*F*
Number of				
Eggs	140.3 ± 10.3	106.3 ± 11.7	74.3 ± 5.9	11.65**
Pupae	175.8 ± 17.5	79.4 ± 13.2	77.8 ± 7.1	17.94**
Imagines	174.9 ± 18.0	77.3 ± 13.3	79.4 ± 7.5	16.80**
Viability				
Egg-pupa	126.3 ± 7.8	73.2 ± 6.8	108.1 ± 5.3	15.68**
Pupa-imago	97.2 ± 5.7	97.1 ± 2.4	103.8 ± 1.5	2.09
Egg-imago	125.3 ± 9.2	70.8 ± 7.4	110.4 ± 5.4	14.90**
Duration of				
Pupation	116.2 ± 9.0	65.9 ± 6.6	119.0 ± 10.5	10.36**
Imagines emergence	115.0 ± 11.2	63.1 ± 6.9	122.2 ± 10.8	10.99**

F for homogeneity of means; **: $P < 0.01$.

Number of females in parentheses.

Table IV - Total fitness index *W'* of the *BR*, *CR* and *TR* strains.

Index	*BR*	*CR*	*TR*
SA'	0.745	3.025	2.038
UI'	0.500	0.382	0.582
I'	2.094	1.879	0.918
P'	8.867	0.136	0.827
W' absolute	6.916	0.295	0.900
relative	1.000	0.043	0.130

SA', *UI'*, *I'* and *P'* respectively for the sexual acitivty, uninseminated females, inseminated females and progeny fractions.

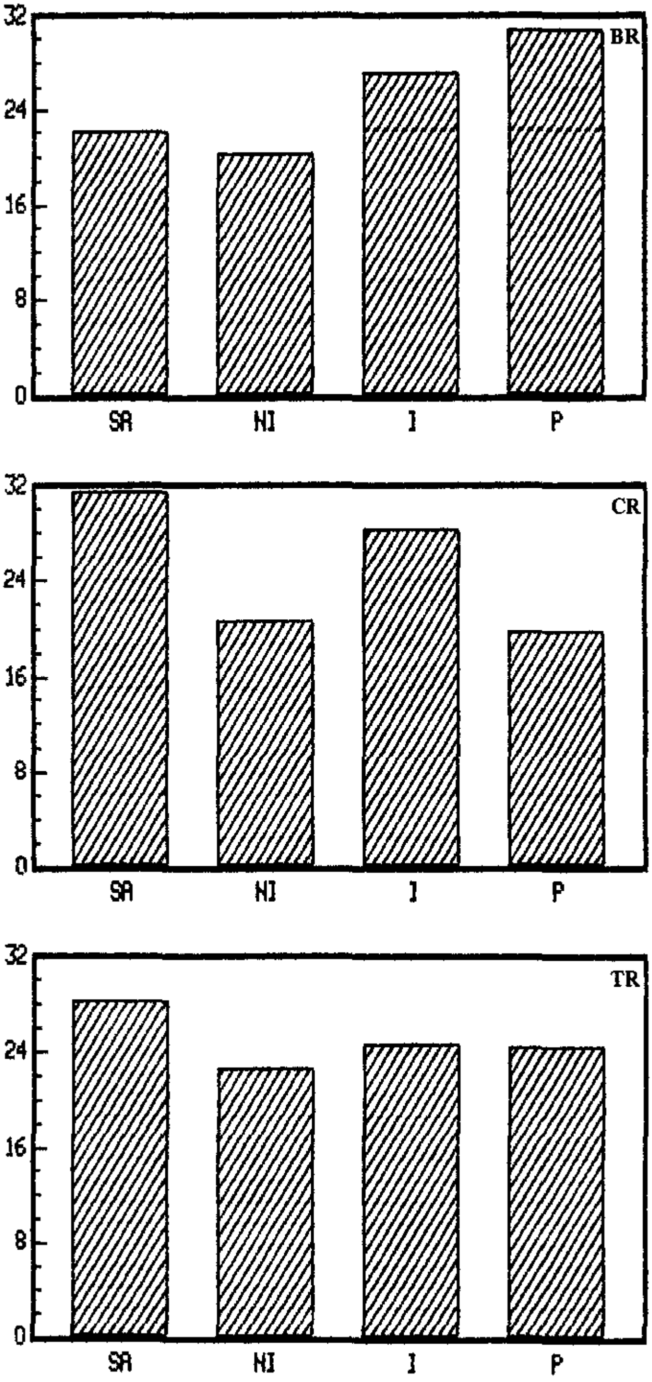

Figure 1 - Relative contribution (in percentage) of fitness fractions for total Darwinian fitness of the *BR*, *CR* and *TR* strains. *SA* - sexual activity, *UI* - uninseminated and *I* - inseminated females and *P* - progeny.

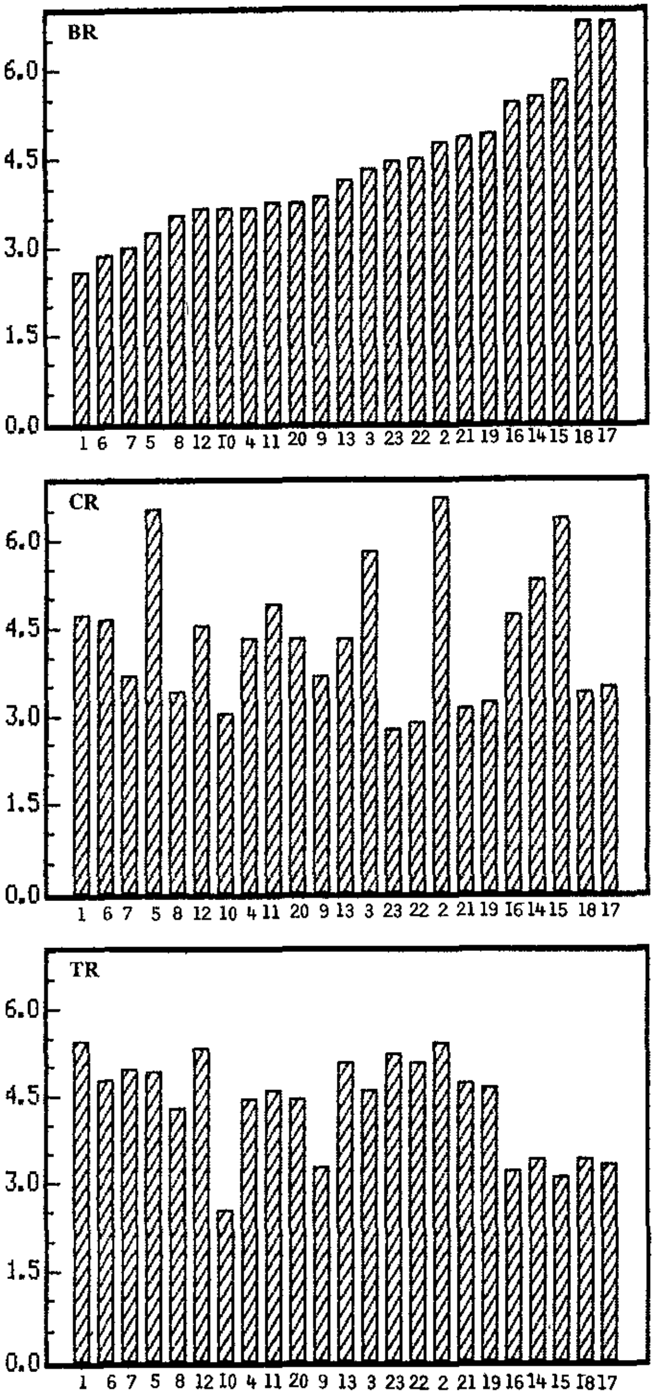

Figure 2 - Relative contribution (in percentage), of the fitness components for total Darwinian fitness of the *BR*, *CR* and *TR* strains. *Sexual Activity* components: *1.* mating frequency, 2. duration of the pre-copula, *3.* absolute duration of the copula, *4.* relative duration of the copula, *5.* time to first copula. *Uninseminated Females* components: *6.* longevity, *7.* absolute duration of the oviposition, *8.* relative duration of the oviposition, *9.* total number of eggs, *10.* daily number of eggs. *Inseminated Females* components: *11.* longevity, *12.* absolute duration of the oviposition, *13.* relative duration of the oviposition, *14.* total number of eggs, *15.* daily number of eggs. *Progeny* components: *16.* number of viable eggs, *17.* number of pupae, *18.* number of imagines, *19.* egg-pupa viability, *20.* pupa-imago viability, *21.* egg-imago viability, 22. duration of pupation, *23.* duration of imagines emergence.

First, correlation analysis was made between pairs of strains. The coefficient computed with the percentual values depicted in Figure 2 gave the following results: -0.051 ($P > 0.05$) for *BR* vs *CR*, -0.100 ($P > 0.05$) for *CR* vs *TR* and -0.518 ($P < 0.01$) for *BR* vs *TR*. The last is shown in Figure 3: excluding the points marked as 9 and 10, corresponding respectively to total and daily number of eggs of uninseminated females, the r value increases to -0.730 ($P < 0.01$); this means that, in general, the fitness components have contrasting importance for the *BR* and *TR* strains.

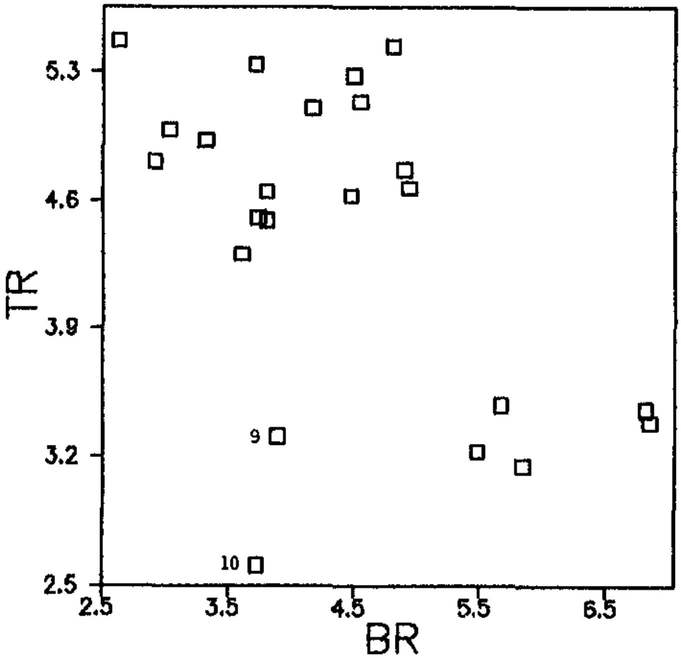

Figure 3 - Correlation between *BR* and *TR* fitness components importance for total fitness. *9* - total and *10* - daily number of eggs of uninseminated females.

Second, by inspection of the graphics, the height of the bars clearly makes it possible to identify some components as of high or low importance for the total fitness of each strain, as follows (numbers as in Figure 2):

Component	*BR*	*CR*	*TR*
1	low	----	high
2	----	high	high
3	----	high	----
5	----	high	----
6	low	----	----
7	low	----	----
9	----	----	low
10	----	low	low
12	----	----	high
14	high	high	low
15	high	high	low
16	high	----	low
17	high	----	low
18	high	----	low
19	----	low	----
21	----	low	----
22	----	low	----
23	----	low	high

Third, also by inspection of the graphics, some components clearly can be identified to have contrasting importance (low, middle or high) in the different strains, as follows (numbers as in Figure 2):

Component	*BR*	*CR*	*TR*
1	low	middle	high
2	middle	high	high
5	low	high	middle
6	high	middle	middle
14, 15	high	high	low
16	high	middle	low
17, 18	high	low	low
22	middle	low	middle
23	middle	low	high

The *W"* method is based on means of each female (Table V). In looking at the *W"* scores, again as with the *W'* ones, it can be seen that *CR* has the highest *SA"*, *TR* the highest *UI"* and the *BR* strain the largest scores of *I"* and *P"*, which shows the consistence of the *W'* and *W"* methods. This fact is powerfully emphasized by the strong positive correlation ($r = 0.779$, $P < 0.01$) between the *AS, UI, I* and *P* scores used in computing *W'* and *W"* (Figure 4); if the point corresponding to *P'* and *P"* of the *BR* strain is excluded, the *r* value increases to an almost perfect correlation of *0.921* ($P < 0.01$).

Table V - Means and standard errors for total fitness index *W"* of the *BR, CR* and *TR* strains.

Index	*BR*	*CR*	*TR*	*F*
SA"	1.099 ± 0.068	1.265 ± 0.084	1.125 ± 0.046	1.70
UI"	0.876 ± 0.094	0.833 ± 0.110	0.924 ± 0.127	0.13
I"	1.182 ± 0.046	1.145 ± 0.058	1.005 ± 0.048	3.20*
P"	1.339 ± 0.092	0.791 ± 0.069	0.994 ± 0.050	14.05**
W" absolute	1.524	0.954	1.038	
relative	1.000	0.626	0.681	

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

SA", *UI"*, *I"* and *P"* respectively for sexual activity, uninseminated females, inseminated females and progeny fractions.

Number of females: for *BR* 20 *SA*, 31 *UI*, 19 *I* and *P*;
for *CR* 32 *SA*, 20 *UI*, 30 *I* and *P*;
for *TR* 38 *SA*, 13 *UI*, 37 *I* and *P*.

DISCUSSION

The essence of the natural selection concept is the differential reproductive efficiency of the genotypes existing in a population. While adaptation or the lack of it expresses itself qualitatively, the degree of adaptation can be determined by quantifying the harmony between organisms and environment. Such quantification can be done through parameters that reflect the population's ability to survive and reproduce in a certain environment. Relative Darwinian fitness measures the probability of survival for the reproduction of a certain genotype, relative to another.

Direct measures of fitness are difficult to obtain, particularly individual fitness. However, the separate measure of fitness components is not difficult and total fitness can be estimated with a combination of their values.

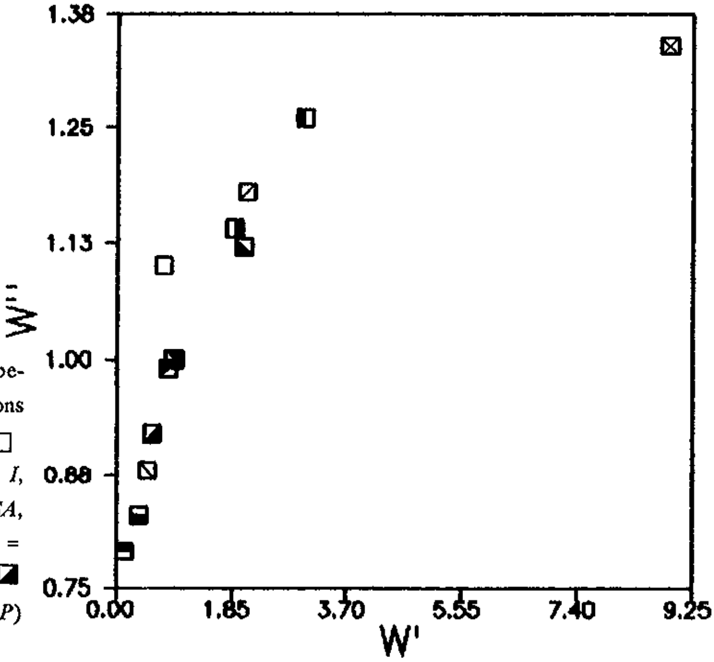

Figure 4 - Correlation between the *W'* and *W''* fractions index values of the *BR* (□ = *SA*, ⧅ = *UI*, ⧄ = *I*, ⊠ = *P*), *CR* (◧ = *SA*, ⬓ = *UI*, ◨ = *I*, ⬒ = *P*) and *TR* (◩ = *SA*, ◪ = *UI*, ◩ = *I*, ◪ = *P*) strains.

Darwinian fitness studies were classified by Hedrick and Murray (1983) on three levels and with four methods. In that it compares the relative fitness of strains differring in all the chromosomes, our study can be classified at the third level. As it takes into account numerous fitness components covering practically the whole biological cycle, our study can also be classified within the fourth method.

Total fitness was dissociated into 23 fitness components, including the fitness fractions sexual activity, inseminated and uninseminated female activity and progeny values. With these measures adaptation indices were calculated.

The adaptation indices *W'* (Table IV) and *W''* (Table V), proposed as representative of total Darwinian fitness, gave evidence for the efficacy of the *BR* strain. Although the *CR* and *TR* strains were more efficient respectively in the sexual activity (Tables I and IV) and the uninseminated female activity (Tables II and IV) fractions, the inseminated female activity (Tables II and IV) and progeny (Tables III and IV) fractions determined the higher *W'* value of *BR*. This last strain was superior to the other two in five progeny components, all related to productivity and viability, probably paramount fitness components for transmitting genes to future generations.

After more than 300 generations in the laboratory, under nearly constant selective pressures, the measure of fitness components and the estimation of the Darwinian fitness through the adaptation indices are a fair indicator of the evolutionary plasticity of the species.

Since *D. prosaltans* is a rare species, with irregular spacial distribution (Dobzhansky and Spassky, 1954), it is probable that the populations present special features influencing their reproductive biology and genetic structure. Thus, the interstrain diversity has to be related to their geographic origin.

Wills (1981) classified fitness components of domestic fowl, cattle and swine in descending order of importance for total fitness. Though based on a subjective evaluation, his attempt, the first ever made, is of critical importance for this nearly unstudied question. In our work, the simple arithmetic procedures used in analysing the data made it possible to establish a hierarchical order of importance for the fitness components. This order differed for the three strains.

Inspection of Figure 2 reveals a remarkable heterogeneity of the three strains. Among the fitness components that varied in terms of importance to total fitness, 11 differs significantly: mating frequency, duration of the pre-copula, time to first copula, longevity, number of eggs (total, daily and viable), number of pupae and imagines, and duration of pupation and of imaginal emergence period. Such variation means different adaptive strategies. If so, it is reasonable to admit a prominent role of these components. A general conclusion is that the relative importance of different components depends on the nature of the biological material and of the experimental conditions.

The methods employed to study the complex problem of estimating Darwinian fitness (W' and W'') and the one for the relative importance of its fractions or components have been shown to be proper and sensible for these purposes and for detecting intra and interstrain variability. The procedures satisfied the necessary conditions for studying total fitness: selection was estimated in practically the whole biological cycle, pre-adult and adult fitness components were not mixed, interactions between components were detected, all selective values were joined in an index, and the relative importance of components and correlated responses were evaluated.

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RESUMO

Este estudo é uma avaliação do valor adaptativo e da importância relativa, para o valor adaptativo total, de 23 componentes de fêmeas de três linhagens de *Drosophila prosaltans* procedentes do Brasil, da Costa

Rica e de Trinidad Tobago, abrangendo praticamente todo o ciclo biológico. O valor adaptativo total foi decomposto em quatro frações eseses(atividade sexual, atividade de fêmeas não-inseminadas e inseminadas, e progênie), as quais foram compostas em dois índices de adaptação W' e W'', propostos como representativos do valor adaptativo total. Os valores das frações esesesatividade de fêmeas inseminadas e progênie, com praticamente todos os componentes relativos a produtividade e viabilidade, determinaram os maiores valores de W' e W'' da linhagem do Brasil. Os componentes estudados mostraram marcadas variações esesesquanto ao seu grau de importância nas três linhagens, evidenciando-se assim estratégias adaptativas diversas. Destacaram-se como mais importantes para a composição do valor adaptativo total a freqüência de acasalamentos, a duração da pré-copula, o tempo para a primeira cópula, a longevidade, o número de ovos (total e diário), de pupas e de imagos e os períodos de duração da pupação e da emergência de imagos. Os métodos empregados para estudar o complexo problema de estimativa do valor adaptativo (W' e W'') e o da importância relativa de suas frações esesesou componentes mostraram-se apropriados e sensíveis para esses propósitos e para detectar variabilidade intra e interpopulacional.

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