DARWINIAN FITNESS IN *Drosophila*. I. FITNESS COMPONENTS OF *Drosophila prosaltans**

Cláudia Márcia Aparecida Carareto and Celso Abbade Mourão[+]

ABSTRACT

The present study is an evaluation of the genetic diversity of three strains of *Drosophila prosaltans*, from Brazil, Costa Rica and Trinidad Tobago. Fifty females of each strain were observed for sexual activity during 60 minutes, and for egg laying and egg development, daily until the death of the flies. A total of 23 fitness components were measured for each strain: five concerned sexual activity (mating frequency, duration of the pre-copula, absolute and relative duration of the copula and the time to first copula), five concerned inseminated and uninseminated female activity (longevity, absolute and relative duration of the oviposition period, and total and daily number of eggs), and eight concerned progeny (number of eggs during the period in which viable eggs were produced, number of pupae and imagines, egg-pupa, pupa-imago and egg-imago viability, and duration of pupation and imaginal emergence period). Differences between the strains for 15 fitness components and for 23 among females of each strain are attributed to intra and interpopulational genetic variability.

INTRODUCTION

The ultimate concern of the evolutionary process is the adaptation of organisms to their environment. The degree of adaptation can be quantified by measuring the parameters involved in the population's ability to survive and reproduce in a certain environment. Darwinian fitness and adaptedness are such parameters (Dobzhansky, 1970).

Natural selection, as a rule, is directed towards the maintenance or enhancement of Darwinian fitness or adaptedness which are a function of the fitness components that operate during the life history of the organisms. Viability, fecundity, developmental rate, sexual activity and longevity are some of these components. An adaptive response to a given environment can be achieved through different combinations of expressions of the fitness components.

Research on this subject has stimulated an abundance of papers, particularly on *Drosophila* species, for which many components have been analysed: these include fecundity, fertility, viability, longevity, productivity, mortality, development rate, intrinsic rate of increase, and population size. However, usually only one component is considered at a time (*e.g.* Anderson and Watanabe, 1968; Polivanov and Anderson, 1969; Simmons *et al.*, 1980 and Brittnacher, 1981), sometimes two (*e.g.* Hiraizumi, 1961; Sved and Ayala, 1970; Mueller and Ayala, 1981 and Rose, 1983) and seldom three (*e.g.* Tantawy and Vetukhiv, 1960; Pyle and Gromko, 1978; Tucic *et al.*, 1981 and Yamazaki and Hirose, 1984). Salceda and Gallo (1975) simultaneously studied nine fitness components.

The experimental procedures designed for this work made it possible to measure 23 fitness components of survival and reproduction in three strains of *D. prosaltans*.

MATERIALS AND METHODS

Three strains of *D. prosaltans*, from Brazil (*BR*), Costa Rica (*CR*) and Trinidad Tobago (*TR*), maintained in our laboratory since 1967, were used. The strains, obtained at the University of São Paulo (USP), originated from the Genetic Foundation of the University of Texas stocks, respectively labelled as *H 2536.9* (Eldorado, RS), *H 400.00* (Palmar) and *H 112.2* (Sangre Grande).

Fifty males and 50 females of each strain, all virgin, were separately aged to nine days. Sets of five couples were observed for sexual activity in transparent plastic boxes nine cm long, six cm wide and three cm high. The number of matings was recorded for each box, as was the beginning and the end of copula for each couple. After 60 minutes of observation the males were discarded and the females were placed individually in vials with banana-agar medium. Each female was then transferred daily to a new vial with fresh food until death. For each female the number of eggs, pupae and emerged imagines was recorded daily. Presence or absence of larvae in the vials was assumed to distinguish inseminated from uninseminated females. For the latter, the number of eggs was also recorded daily. Eventually the inseminated

females laid eggs that did not produce larvae, which nevertheless continued to be counted. The experiments were carried out in a 25°C constant temperature room.

The five sexual activity measures were: (1) the duration of the pre-copula, taken as the time interval between the beginning of the observation in the mating box and the beginning of copula; (2) the absolute duration of the copula, taken as the time during which the male remained over the female; (3) the relative duration of the copula, which is the absolute duration of the copula as a percentage of the pre-copula plus copula duration; (4) the time to first copula in each mating box; and (5) the mating frequency. The time unit for (1), (2) and (4) was minutes.

Five additional measures of each female were made on inseminated and uninseminated females: (1) longevity, in days; (2) the absolute duration of the oviposition period, taken as the number of days between the beginning and the end of the oviposition period; (3) the relative duration of oviposition period, taking the absolute oviposition period as a percentage of longevity; (4) the total number of eggs; and (5) the daily number of eggs, taken as the ratio between the total number of eggs and days of oviposition.

For the progeny of each inseminated female the eight measures were: the number of (1) eggs, (2) pupae and (3) imagines; (4) egg-pupa, (5) pupa-imago and (6) egg-imago viability, respectively taken as the pupa/egg, imago/pupa and imago/egg quotients, times 100, calculated according to the number of eggs laid during the period in which viable eggs were produced; and duration of the (7) pupation and (8) imaginal emergence period, taken respectively as the number of days between the first and the last appearance of pupae and imagines.

RESULTS

The duration of the study was 79, 88 and 106 days, for the females from the *BR, CR* and *TR* strains, respectively.

The longevity of inseminated compared to uninseminated females (Table I) was significantly greater only in the *BR* strain ($t = 2.17; P < 0.01$). When the strains were compared, F values from the analysis of variance were significant ($P < 0.01$), except for among inseminated females. The lowest longevity was that of the *BR* strain and those of the other two were about equal.

Sexual activity exhibited a clear heterogeneity among the three strains for three of the four components (Table II). Significant differences for the time to first copula ($F = 4.92; P < 0.01$) and the duration of copula ($F = 7.36; P < 0.01$) were observed. The mating frequency was 40%, 64% and 76%, respectively for the *BR, CR* and *TR* strains (chi-square $= 14.00; P < 0.01$).

Table I - Means and standard errors of longevity of the *BR, CR* and *TR* strains.

Strain	Uninseminated females	Inseminated females	t	All females
BR	40.4 ± 3.8 (31)	52.4 ± 3.6 (19)	2.17*	45.0 ± 2.8
CR	56.6 ± 4.2 (20)	59.8 ± 3.6 (30)	0.58	58.5 ± 2.7
TR	60.0 ± 7.6 (13)	58.1 ± 4.2 (37)	0.23	58.6 ± 3.7
F	5.31**	0.68		6.44**

F for homogeneity of means.
t for the differences between means.
*: $P < 0.05$; **: $P < 0.01$.
Number of females in parentheses.

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

Strain	Pre-copula	Time to 1st copula	Copula	
			Absolute	Relative
BR (20)	27.2 ± 2.6	22.7 ± 3.6	18.4 ± 0.9	42.6 ± 2.2
CR (32)	26.4 ± 2.6	12.9 ± 1.8	16.9 ± 0.8	43.8 ± 2.9
TR (38)	27.9 ± 2.3	14.0 ± 0.8	23.1 ± 1.5	46.8 ± 3.0
F	0.10	4.92**	7.36**	0.53

F for homogeneity of means; **: $P < 0.01$.
Number of females in parentheses.

Total and daily numbers of eggs laid (Table III) were lower in uninseminated compared to inseminated females. The small Student t values are due to the enormous variances, since the number of eggs per female in the three strains ranged from zero to between 130 and 240. Both the total and the daily number of eggs of both uninseminated and inseminated females increase in the order $TR < CR < BR$. The four homogeneity F values are significant, except for the total number of eggs of uninseminated females.

Table III - Means and standard errors of total and daily number of eggs of uninseminated (*UI*) and inseminatd (*I*) females of the *BR, CR* and *TR* strains.

Strain		Total	*t*	Daily	*t*
BR UI	(31)	72.2 ± 12.1		2.1 ± 0.2	
I	(19)	103.6 ± 7.0	1.91	3.3 ± 0.4	2.93**
CR UI	(20)	60.2 ± 12.4		1.5 ± 0.2	
I	(30)	87.0 ± 7.6	1.95	3.1 ± 0.5	2.50*
TR UI	(13)	55.4 ± 11.8		1.3 ± 0.2	
I	(37)	58.3 ± 4.3	0.30	1.6 ± 0.1	1.05
F UI		0.46		3.27*	
I		13.38**		7.46**	

F for homogeneity of means.

t for the differences between means.

*: $P < 0.05$; **: $P < 0.01$.

Number of females in parentheses.

The number of eggs laid in the fertile period and the number of pupae and imagines are given in Table IV. Although the increasing order $TR < CR < BR$ was maintained as for the eggs, the pupa and imago order may be written as $TR = CR < BR$, the means for this last strain being exceedingly higher than those of the other two. For the three sets of means the *F* values are significant ($P < 0.01$).

Table IV - Means and standard errors of number of viable eggs, pupae and imagines of the *BR, CR* and *TR* strains.

Strain	Eggs	Pupae	Imagines
BR (19)	98.5 ± 7.1	76.4 ± 7.6	68.0 ± 7.0
CR (30)	74.6 ± 8.2	34.5 ± 5.7	30.1 ± 5.2
TR (37)	52.1 ± 4.2	33.8 ± 3.1	31.0 ± 2.9
F	11.65**	17.93**	16.81**

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

Number of females in parentheses.

The viability data (Table V) can be summarized as follows: while an increasing order $CR < TR < BR$ was observed for egg-pupa and egg-imago viability, the three strains presented about the same value for pupa-imago viability. This is confirmed by the F values from analysis of variance ($P < 0.01$).

Table V - Means and standard errors of egg-pupa, pupa-imago and egg-imago viability of the *BR, CR* and *TR* strains.

Strain	Egg-pupa	Pupa-imago	Egg-imago
BR (19)	76.0 ± 4.7	85.6 ± 5.0	67.3 ± 4.9
CR (30)	44.1 ± 4.1	85.5 ± 2.1	38.3 ± 4.0
TR (37)	65.2 ± 3.2	91.5 ± 1.3	59.3 ± 2.9
F	15.67**	2.11	14.56**

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

Number of females in parentheses.

The duration of the oviposition period is shown in Table VI. Both the absolute and relative values are lower in uninseminated than in inseminated females for each strain, but the means are not significantly different (Student t probabilities are above 0.05). Taking the face values of both kinds of females the absolute duration of the oviposition period increases in the order $BR < CR < TR$; however, the four F values are not significant, except for the relative duration of the oviposition period of inseminated females ($F = 5.41; P < 0.01$). The pupation and imaginal emergence period (Table VI) were pronouncedly different among the strains, with highly significant F values ($P < 0.01$). For both the pupation and the imaginal emergence period the order may be written as $BR = TR > CR$, the means of the last strain being almost half of the other two.

Figure 1 reflects four striking differences between the strains. The first is the duration of the oviposition period, 10, 11 and 14 weeks, and the second is the imagines emergence period of five, three and seven weeks, respectively for *BR, CR* and *TR* females. Third, nearly all the *BR* flies emerged in two weeks, while those of the other two strains did so in only one. Finally, the three strains can be discriminated by the weekly pattern of oviposition, which was about the same for uninseminated and inseminated females within the same strain.

Table VI - Means and standard errors of duration of the oviposition, pupation and imaginal emergence period of uninseminated (*UI*) and inseminated (*I*) females of the *BR*, *CR* and *TR* strains.

Strain		Oviposition		Pupation period	Imaginal emergence period
		Absolute	Relative		
BR UI	(31)	28.1 ± 3.6	56.7 ± 5.6		
I	(19)	34.5 ± 2.8	65.7 ± 2.7	21.4 ± 1.6	20.5 ± 2 0
CR UI	(20)	30.0 ± 5.1	47.4 ± 7.2		
I	(30)	37.1 ± 3.6	60.1 ± 3.6	12.1 ± 1.2	11.2 ± 1.2
TR UI	(13)	42.1 ± 8.2	61.3 ± 8.0		
I	(37)	45.1 ± 4.4	73.0 ± 2.3	21.9 ± 1.9	21.8 ± 1.9
F UI		1.73	0.91		
I		1.84	5.41**	10.34**	10.99**

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

Number of females in parentheses.

A correlation analysis was performed with the parameters studied. Out of 17 *r* coefficients calculated, 11 were concordant in the three strains. Three of them showed lack of correlation: between copula and pre-copula duration and between egg-imago viability and number of eggs, daily and total. A negative correlation of 0.6 ($P < 0.01$) was found between the daily number of eggs laid and the abolute duration of the oviposition period of inseminated females. Five strong positive correlations, above 0.8 ($P < 0.01$), were found: between the number of viable eggs and the number of pupae or imagines; between the number of pupae and that of imagines; between the pupation and imaginal emergence period; and between the total number of eggs and the absolute duration of the oviposition period of the uninseminated females. The egg-imago viability was also positively correlated with the number of imagines at the 1% level, but the *r* values were between 0.5 and 0.7. Finally, the absolute duration of the oviposition period and longevity were also positively correlated but the *r* values varied from 0.5 ($P < 0.05$) for *BR* to 0.8 and 0.98 ($P < 0.01$), respectively for the *CR* and *TR* strains.
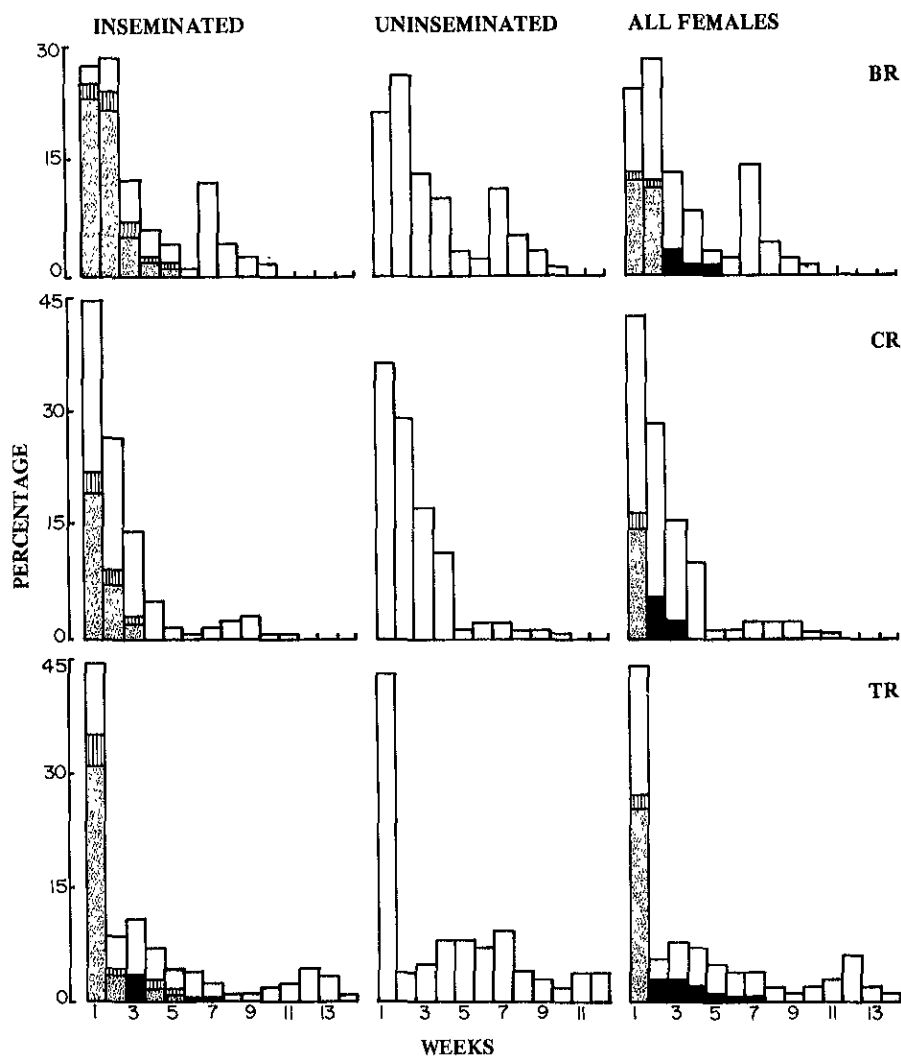
Figure 1 - Weekly production of eggs, pupae and imagines of the *BR, CR* and *TR* strains. Open = eggs, hatched = pupae, dotted = imagines and black = (approximately equal number of) pupae and imagines.

The three strains did not agree in six correlations. The *r* values, between 0.4 and 0.6 ($P < 0.01$), were significant for the *TR* strain only, between the absolute duration of the oviposition period and the total number of eggs of inseminated females or duration of the imaginal emergence period; between the relative duration of the

oviposition period and longevity and between the mating duration (copula plus pre-copula) and the relative duration of the copula. In the *BR* and *CR* strains only, with *r* values ranging from 0.5 to 0.8 ($P < 0.01$) between the absolute duration of the oviposition period and the daily number of eggs of uninseminated females. These results indicate that the *BR* and *CR* strains are more similar to each other, than to the *TR* strain. Finally, a relatively weak positive correlation, around 0.4 ($P < 0.05$), occurred in the *BR* and *TR* strains, compared with a lack of correlation in the *CR* strain between the absolute duration of the oviposition period and the duration of the pupation period.

DISCUSSION

The measurement of Darwinian fitness is a permanent challenge in evolutionary biology research. Two different kinds of experiments have been designed to approach this task. In a first approach the few population studies for the estimation of total fitness (*e.g.* Sved and Ayala, 1970; Mourão *et al.*, 1972; Wilton and Sved, 1979 and Polivanov, 1981) can be included. On the other hand there are numerous studies involving several fitness components. This paper, as a third kind of experiment is an attempt to simultaneously study many fitness components, through analysis of a relatively small sample of 150 females. As was pointed out by Dobzhansky (1968), the adaptive value of a genotype varies in different environmental conditions which change in time and space.

Our investigation of sexual activity made apparent a pronounced heterogeneity among the strains for relevant components of mating success: mating frequency, the time to first copula and the absolute duration of the copula (Table II). Mating frequency, in experimental situations, is determined by the number, time of exposition and age of couples (Spiess and Spiess, 1969). In this work, the couples were nine days old, the age at which the three strains present the highest mating frequency values (Buzini, 1973). If the duration of the copula really means an advantage for the faster flies (Parsons and Kaul, 1966), the *TR* strain should be in disadvantage compared to *BR* and *CR*, however this disadvantage is balanced by a higher mating frequency.

Diversity among the strains becomes evident when longevity, insemination and fecundity are considered together. Maynard Smith (1958) verified a greater survival of *D. subobscura* virgin females than of inseminated ones. The same result was obtained by Malick and Kidwell (1966) in *D. melanogaster*; nevertheless, this relation was not corroborated by the same authors, also with *D. melanogaster* (Kidwell and Malick, 1967). In view of this, Lamb (1978) deduced that the relationship between these components are intricate and a general conclusion can not be stated. In this

study, the *BR* inseminated females showed a greater longevity than uninseminated ones, but for the other two strains the difference was not significant (Table I). The disagreements could be due to the experimental procedures or to the inherent diversity of the *Drosophila* species studied.

A negative association between longevity and number of eggs (Tables I and III), also found by Lamb (1964) in *D. melanogaster*, may be a consequence of the reproductive effort (Fisher, 1930). However this also could be a result of an adjustment mechanism of the strains, such as the less productive flies remaining longer in the environment, thus controlling population size.

The *TR* strain had the longest fertile period and greatest mating frequency, both about twice the lowest values found, but together with *CR* it presented the lowest fecundity and number of imagines. This last strain also had the highest mating speed (the smallest duration of pre-copula), the shortest time to first copula, and a mating frequency higher than that of the *BR* strain, and had a lower fecundity and the lowest number of imagines (Tables II and IV).

The meaning of the correlation analysis results is not easily understood. Perhaps these data should be listed together with the many *r* values obtained by other authors (*e.g.* Hiraizumi, 1961; Watanabe and Oshima, 1973; Giesel and Zettler, 1980; Petit *et al.*, 1980 and Yamazaki, 1984). Agreements and disagreements are equally common. It is possible that the correlation analysis values simply reflect particularities of the different species as well as the environmental conditions of the experiments.

These results corroborate Dobzhansky's (1974) assertion that "natural selection promotes the establishment of genetic variants with some disadvantageous features that are more than compensated by advantages in other features". They also show that the three strains have different adaptive strategies which could be due to their genetic diversity and geographic origin.

RESUMO

Este trabalho é uma avaliação da diversidade genética de três linhagens de *Drosophila prosaltans*, do Brasil, da Costa Rica e de Trinidad Tobago. De 50 fêmeas de cada linhagem, observou-se a atividade sexual durante 60 minutos e, diariamente até a morte das moscas, a oviposição e o desenvol-

vimento dos ovos. Para cada linhagem, foram medidos 23 componentes do valor adaptativo: cinco da atividade sexual (freqüência de acasalamentos, tempos de pré-cópula, para a ocorrência da primeira cópula e de cópula, absoluto e relativo), cinco relativos à atividade de fêmeas inseminadas ou não (longevidade, duração do período de oviposição, absoluto e relativo, e número de ovos, total e diário), e oito da progênie (número de ovos do período fértil, no qual foram produzidos ovos viáveis, de pupas e de imagos, viabilidade ovo-pupa, pupa-imago e ovo-imago, e duração do período de pupação e de emergência dos imagos). Diferenças observadas entre as linhagens para 15 componentes e entre as fêmeas de cada linhagem para os 23 foram atribuídas à variabilidade genética intra e interpopulacional.

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