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PRODUCTIVITY IN MASS CROSSES OF *Drosophila sturtevanti*: A COMPARATIVE STUDY OF LABORATORY STOCKS AND RECENTLY COLLECTED FLIES*

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ABSTRACT

Drosophila sturtevanti from several geographic origins were analyzed for their capacity to intercross and to yield progeny. Mass intercrosses involving laboratory stocks and recently collected strains were fertile, which suggests that the genetic differentiation among these geographically isolated populations did not affect their reproductive patterns sufficiently to lead to reproductive isolation. Analysis of the number of progeny (productivity) in intracrosses and intercrosses was informative as to the amount of variation this feature exhibits in the laboratory stocks and in the recently collected strains. Also laboratory stocks and recently collected flies shared a positive correlation in that the greater the control productivity of a strain the greater the number of its intercrosses which exhibited reduced productivity.

INTRODUCTION

Reproductivity strategy is certainly one of the basic features in the success of a population facing selective forces. The great variability presented by natural populations is indicative that each species is probably unique relative to both the kind of elements which are involved in this strategy and the way such elements are combined.

Drosophila sturtevanti from several geographic origins have been analyzed in our laboratory for their capacity to intercross and yield progeny. The study of this species is pertinent since it has a wide geographic distribution (from Mexico to the South of Brazil and Paraguay), the widest among species in the Saltans group, and because it is relatively ease to collect, favoring studies of local populations.

In the present paper, data on strains kept in laboratory for long periods are compared with data on recently collected flies. This approach was used to determine if laboratory conditions interfere with this parameter.

MATERIAL AND METHODS

Twenty-four strains maintained under laboratory conditions from seven to 21 years and 67 isofemale lines (derived from single, recently collected females, inseminated in nature) from 11 different geograhic origins were used in this study.

Symbols and geographic origins of the laboratory strains are in Table I. Most were obtained from stocks of the Genetics Foundation of the University of Texas, Austin, USA, and from stocks of the University of São Paulo, Brazil.

Symbols and geographic origins of recently collected flies and the number of isofemale lines obtained from each origin are in Table III. They were analyzed at the most six months after capture in nature.

For both laboratory and recently collected flies, mass crosses on banana-agar culture medium were made. These involved 10 pairs of virgin, five day old flies in both crossing directions. For laboratory stocks, a single bottle was prepared, for each type of intracross (controls) or intercross, the flies being transferred to bottles with new culture medium at four day invervals, once (if they

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produced progeny in the first bottle) or twice (if they did not produce progeny in the first bottle).

In the case of mass intercrosses involving recently collected flies, two replicas were prepared for every combination in both crossing directions and flies were transferred to bottles with new culture medium at four day intervals. Mass intercrosses were also used as controls.

Isofemale lines of the same samples were mass crossed following the chain method used by Dobzhansky *et al.* (1964). According to this method, three types of crosses are made if a collected sample originates three isofemale lines. If these isofemale lines are designated A, B and C, the chain crosses will be AxB, BxC and CxA. In the chain cross technique, isofemale lines from the same origin which intercross freely may be joined to form a strain. In the present study these strains were prepared by taking 100 flies from every isofemale line from the same origin, combining all in a single bottle and distributing them among three new bottles.

In every case, the analysis was performed 30 days after the cross preparation. Fertility (presence or absence of progeny) and productivity (number of descendants in F1) were computed.

RESULTS

A. Laboratory flies

All 552 mass intercrosses resulting from combining the 24 laboratory stocks were fertile, most showing numerous progeny. However, by grouping crosses involving females from the same strain, a great variation in productivity was observed.

Table I shows the productivity of the controls (intracrosses of each strain), mean productivity of all types of intercrosses involving females from the same strain, as well as minimum and maximum values for this productivity. Variation in productivity among intercrosses involving females of the same origin was great, with differences between the minimum and maximum values that varied from 339 descendants (strain K-75) to 845 descendants (strain 86).

Table I - Laboratory strains. Productivity (number of progeny) of intracrosses (controls) and mean productivity of intercrosses involving females from the same orgin. Strains are listed in decreasing order of control productivity.

Strain	Geographic origins	Control	Intercrosses		
			Mean	Mimimum	Maximum
BG_3	Guiana	692	450	59	791
TRIN	Trinidad	617	457	241	906
IP	Campo Grande (MS), Brazil	566	493	228	769
126	Colombia	555	427	49	751
ST-L	Jamaica	553	441	156	839
98	Itatiaia (RJ), Brazil	520	482	150	813
133	Turrialba, Costa Rica	508	486	175	811
TAP	Tapuruquara (AM), Brazil	500	443	156	837
97	Belém (PA), Brazil	470	544	178	838
BG_7	Guiana	466	467	173	754
93	Ilha das Cobras (RJ), Brazil	461	595	142	909
OL	Olimpia (SP), Brazil	432	478	183	828
RB	Litoral Rio-Bahia, Brazil	415	436	183	609
MIR	Mirassol (SP), Brazil	409	390	149	682
92	Manaus (AM), Brazil	391	438	186	697
VC	Vera Cruz, Mexico	333	523	221	745
108	El Yunque, Porto Rico	308	450	187	789
89	Goiania (GO), Brazil	307	376	117	717
RP	São J.R. Preto (SP), Brazil	305	394	59	812
MAN_2	Manaus (AM), Brazil	278	427	149	835
86	Maraba (PA), Brazil	258	625	254	1099
91	Sacavem (AM), Brazil	225	420	145	708
69	Panama	213	561	199	967
K-75	Guaruja (SP), Brazil	151	389	190	529

Table II shows the percentage distribution of productivity variation for all intercrosses involving females from the same laboratory stock in relation to their control. Among the 552 combinations 218 showed a productivity increase and 334 a productivity decrease. Strains which had the greatest control productivities in general showed a productivity decrease in most of their intercrosses and vice-versa.

B. Recently collected flies

Data on productivity for the recently collected samples are in Table III. Mean productivity of each sample was calculated by summing the mean productivity of both replicas of all intracrosses of isofemale lines from the same sample and dividing by their number, except for samples MAN and NI, which gave a single isofemale line each.

Mean productivity of isofemale lines in each sample varied considerably. Isofemale lines from samples A60 and A88 presented the lowest minimum productivity values while the highest maximum values were presented by isofemale lines from samples A60, A63 and CE. Greatest amplitude was found in the isofemale lines from sample A60, with a maximum value five times greater than the minimum value. Smallest amplitude was found in the sample A69, with a maximum value which was less than the double the minimum value.

Considering samples with more than one isofemale line, 52 or 80% presented significant differences between replicas, most of them (43 or 64%) at the $P < 0.005$ level (Chi-square test).

Productivity of chain intercrosses of isofemale lines in each sample and mean productivity of intercrosses (links) in each direction are presented in Table IV. In every

Table II - Laboratory strains. Distribution of productivity variation among all intercrosses involving females from the same strain in relation to their control. Number of combinations given in parentheses.

Strain	Productivity variation in relation to control													
	% Decrease						% Increase							
	0-10	11-30	31-50	51-70	71-100		0-10	11-30	31-50	51-70	71-100	101-300	+300	
BG_3	1	1	11	4	1	(18)	3	2	-	-	-	-	-	(5)
TRIN	2	8	9	2	-	(21)	-	1	1	-	-	-	-	(2)
IP	1	8	3	3	-	(15)	2	5	1	-	-	-	-	(8)
126	2	3	5	5	1	(16)	3	2	2	-	-	-	-	(7)
ST-L	4	7	2	4	1	(18)	4	-	-	1	-	-	-	(5)
98	1	6	2	2	1	(12)	3	5	2	1	-	-	-	(11)
133	3	4	4	2	-	(13)	2	3	4	1	-	-	-	(10)
TAP	2	5	4	4	-	(15)	2	3	1	2	-	-	-	(8)
97	2	2	1	1	-	(6)	2	9	3	2	1	-	-	(17)
BG_7	1	6	2	2	-	(11)	4	3	2	2	1	-	-	(12)
93	1	1	1	1	-	(4)	2	5	5	4	3	-	-	(19)
OL	3	2	2	1	-	(8)	3	6	2	3	1	-	-	(15)
RB	1	4	-	2	-	(7)	7	3	6	-	-	-	-	(16)
MIR	2	8	3	1	-	(14)	3	2	3	1	-	-	-	(9)
92	2	4	2	1	-	(9)	1	6	2	3	2	-	-	(14)
VC	2	-	1	-	-	(3)	-	3	5	3	5	4	-	(20)
108	2	1	1	-	-	(4)	1	4	1	5	6	2	-	(19)
89	3	1	2	2	-	(8)	2	4	3	3	-	3	-	(15)
RP	2	2	-	3	-	(7)	1	4	2	4	3	2	-	(16)
MAN_2	2	-	2	-	-	(4)	2	3	4	-	7	3	-	(19)
86	1	-	-	-	-	(1)	1	-	-	2	3	15	1	(22)
91	2	1	1	-	-	(4)	2	1	2	1	2	11	-	(19)
69	1	-	-	-	-	(1)	1	-	-	1	4	14	2	(22)
K-75	-	-	-	-	-	(0)	-	2	-	1	2	18	-	(23)
Total	43	74	60	40	4	218	51	76	51	40	40	72	3	334

Table III - Recently collected samples. Geographic origin, number of isofemale lines yielded by each sample (in parentheses) and productivity of isofemale line intracrosses presented in decreasing order.

Sample		Geographic origins	Productivity		
			Mean	Minimum	Maximum
A_{63}	(14)	Fazenda Palmital (PR), Brazil	561	336	843
A_{60}	(10)	Mogi Guaçu (SP), Brazil	454	161	847
A_{88}	(10)	São Carlos (SP), Brazil	381	181	666
B_{10}	(8)	Caracas, Venezuela	514	274	744
CE	(7)	Pacatuba (CE), Brazil	648	473	840
A_{68}	(5)	Fazenda Água do Índio (PR), Brazil	474	239	761
JAND	(4)	Fazenda Jandaia (SP), Brazil	455	237	581
A_{69}	(4)	Rio Ligeiro (PR), Brazil	512	392	706
A_{59}	(3)	Praia de Utinga (PR), Brazil	457	240	644
MAN	(1)	Manaus (AM), Brazil	458*	-	-
NI	(1)	Nova Itapirema (SP), Brazil	341*	-	-

*A single isofemale line productivity.

Table IV - Recently collected samples. Productivity of chain crosses of isofemale lines and mean productivity of links (crosses) in each direction. F = females; M = males.

Sample	Crossing direction	Productivity of chain crosses (links)														
		A-B	B-C	C-D	D-E	E-F	F-G	G-H	H-I	I-J	J-K	K-L	L-M	M-N	N-A	Mean
A_{63}	F x M	686	469	426	1043	836	372	631	741	906	942	671	989	776	1352	774
	M x F	738	445	589	878	402	810	359	989	541	713	1094	1241	1507	555	776
A_{60}	F x M	753	826	1069	298	1087	896	816	456	710	552					746
	M x F	592	769	601	395	674	339	585	693	493	700					584
A_{88}	F x M	448	885	1320	339	1086	427	630	689	943	990					776
	M x F	674	743	711	941	698	461	473	724	443	792					666
B_{10}	F x M	418	988	661	1132	499	470	1352	1103							828
	M x F	854	477	648	623	564	652	540	1223							698
CE	F x M	807	810	1125	638	869	564	485								757
	M x F	591	663	1071	517	786	570	591								684
A_{68}	F x M	656	584	895	1133	238										701
	M x F	925	788	486	508	248										591
JAND	F x M	787	732	928	763											802
	M x F	829	675	599	391											623
A_{69}	F x M	563	532	720	894											677
	M x F	654	648	799	557											664
A_{59}	F x M	461	1009	482												651
	M x F	576	597	513												562

link, productivity was obtained by summing values of both replicas.

Sterile links were not found, but productivities varied greatly along the chain, in every sample, showing in subsequent links a decrease or increase in both crossing directions or a decrease in one direction and an increase in the other. In general, when the productivity of one link was up to 1000 descendants, the next link exhibited a productivity decrease.

A comparison of the mean productivity of isofemale line intracrosses (Table III) with the mean productivity of isofemale line intercrosses in each sample (Table IV) showed that the second are greater than the first in every case.

In chain intercrosses, 71% of the total of 130 combinations showed significant differences in productivity, most (73 links or 56%) at the $P < 0.005$ level.

Crosses involving females from strains A68, NI, A59 and B10 showed the lowest minimum productivities. Tree of them (NI, A59 and B10) are among the strains with greatest amplitudes, showing that variability in the number of progeny among intercrosses of females from the same strain was high. Greatest productivities of recently collected strains were presented by MAN, JAND, NI and A88 (Table V).

As was also found in laboratory strains, recently collected strains exhibiting the highest control productivities also exhibited decreased productivity in most of their intercrosses and vice-versa. Of the total of 110 combinations of crosses, 60% showed a productivity decrease (Table VI). Thus mass crosses of both laboratory stocks and recently collected strains behaved the same in this respect.

Table V - Recently collected strains. Productivity of intracrosses (controls) and productivity of intercrosses involving females from the same origin. Strains are in decreasing order of control productivity.

Strain	Productivity			
	Control	Intercrosses		
		Mean	Minimum	Maximum
*MAN	477	334	154	682
*NI	319	280	91	520
A59	289	275	95	459
A63	341	253	143	355
CE	277	231	113	341
A69	355	230	147	363
A68	251	184	81	288
A88	252	328	135	502
JAND	280	308	145	569
B10	225	241	96	448
A60	206	219	140	315

*A single isofemale lines analyzed.

Table VI - Recently collected strains. Percentage distribution of productivity variation among intercrosses involving females from the same strain in relation to their control. Number of combinations given in parentheses.

Strain	Productivity variation in relation to control												
	% Decrease						% Increase						
	0-10	11-30	31-50	51-70	71-100		0-10	11-30	31-50	51-70	71-100	+100	
MAN	-	4	3	2	-	(9)	-	-	1	-	-	-	(1)
A69	-	2	3	4	-	(9)	1	-	-	-	-	-	(1)
A63	1	6	1	1	-	(9)	1	-	-	-	-	-	(1)
NI	-	3	2	-	-	(5)	2	1	-	1	1	-	(5)
A59	-	3	2	1	-	(6)	-	2	2	-	-	-	(4)
JAND	2	-	3	-	-	(5)	-	3	-	-	1	1	(5)
CE	-	2	3	1	-	(6)	2	2	-	-	-	-	(4)
A88	1	-	1	-	-	(2)	-	4	2	-	2	-	(8)
A68	2	1	3	1	1	(8)	1	1	-	-	-	-	(2)
B10	-	3	-	1	-	(4)	1	4	-	-	1	-	(6)
A60	1	1	1	-	-	(3)	2	4	-	1	-	-	(7)
Total	7	25	22	10	1	(66)	10	21	5	2	5	1	(44)

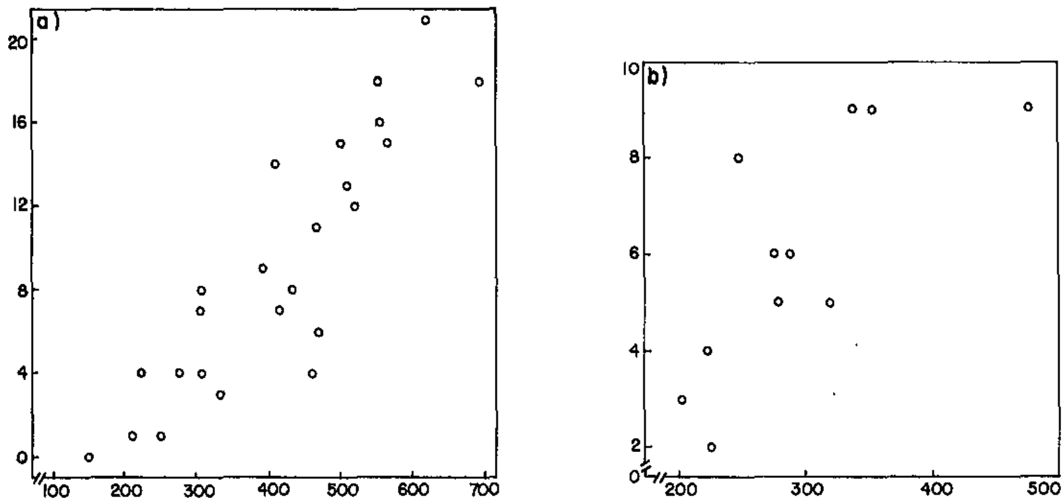

Figure 1 - Correlation between productivity of the controls (number of the flies in abcissa) and the frequency of intercrosses of each strain with productivity smaller than that of the respective control (number of crosses in ordinate). a. Laboratory strains; b. Recently collected strains.

There was a positive and significant correlation between control productivity of each laboratory strain (Figure 1a) or each recently collected strain (Figure 1b) and the frequency of combinations involving each strain which exhibited a number of progeny smaller than the control (for laboratory strains, $r = 0.719$, $t_9 = 3.103$, $P < 0.005$; for recently collected strains $r = 0.828$, $t_{22} = 8.815$, $P < 0.001$).

DISCUSSION

All mass intercrosses involving laboratory stocks and recently collected strains were fertile indicating that the genetic differentiation occurred among geographically isolated *D. sturtevanti* populations did not affect their reproductive patterns sufficiently to lead to reproductive isolation.

In the laboratory stocks as well as in the recently collected strains, productivity varied greatly among strains (control productivities), among intercrosses of different strains and even among different intercrosses involving females of the same strain.

In the recently collected samples, productivity also varied among isofemale lines from the same sample and between replicas of the same intercross.

Productivity is a complex character, involving the segregation of several mendelian loci (perhaps polygenic loci too) which affect different reproductive aspects. The sources of variation for productivity are very numerous and interaction of alternative genotypes may lead to different responses even in intrastrain and intra isofemale lines, as detected in the present paper. Besides, data in literature has shown that genetic background also plays an important role in productivity variation. In *D. melanogaster*, fecundity, understood as the number of eggs produced per fly per day, is apparently controlled by a dominant factor located on chromosome III, but the degree of dominance seems to be dependent on the background heterozigosity (Domingues and Rubio, 1986, apud Kilias *et al.*, 1989).

Besides a high degree of productivity variation, the laboratory stocks and the recently collected flies of *D. sturtevanti* shared a positive correlation between productivity of each strain and the frequency of combinations involving that strain which exhibited a number of progeny smaller than that of the control. Strains with high control productivity probably already carry selected genic combinations for high performance for this feature and in a mixture with other gene pools the probability of weakening them is greater than of improving them. On the contrary, strains with low productivity have combinations easily liable to be improved when mixed in hybrids.

The great variability found in the laboratory stocks, as well as in the recently collected strains of *D. sturtevanti* indicates that despite the laboratory conditions under which the strains are submitted to some degree of inbreeding and perhaps to genetic drift (as mentioned by David *et al.*, 1978, apud Cohet and David, 1980) they still preserve variability for productivity.

Singh and Chatterjee (1987) found significant variation in fertility among five isofemale lines of *D. ananassae* from different geographic localities, which had gone through numerous generations (more than 12 years) in the laboratory. For those authors, variability observed seems to be attributable to the genetic heterogeneity among the isofemale line founders.

In spite of the similarity between laboratory stocks and recently collected strains of *D. sturtevanti* relative to productivity, described in the present paper, the occurrence of some effects derived from maintenance of this species in laboratory cannot be discarded.

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RESUMO

Drosophila sturtevanti proveniente de localidades diferentes foi analisada quanto à capacidade de intercruzamento e produção de progênie. Intercruzamentos em massa de estoques de laboratório e de linhagens recém-coletadas foram férteis mostrando que a diferenciação genética entre essas populações, geograficamente isoladas, da espécie, não afetou seus padrões reprodutivos suficientemente para levar ao isolamento reprodutivo. A análise do número de descendentes (produtividade) em intra e intercruzamentos foi informativa sobre a quantidade de variação apresentada por essa característica, tanto nos estoques de laboratório como nas recém-coletadas. Estoques de laboratório e moscas recém-coletadas partilham também uma correlação positiva segundo a qual quanto maior a produtividade controle de uma linhagem, maior o número de seus intercruzamentos com produtividade reduzida.

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