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Competition studies in *Drosophila*: Relative fitness and adaptedness of six closely related species

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Abstract. Inter and intra specific competition experiments involving 6 taxonomically closely related forms of *Drosophila* have been made. Relative fitness and adaptedness of these forms have shown different levels indicating a lack of correlation between taxonomic proximity and ecological phenotype.

Keywords. Drosophila; competition; fitness.

1. Introduction

'As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution and always in structure, the struggle will be more between them, if they come into competition with each other than between the species of distinct genera' (Darwin 1859). The understanding of the competitive relationships between closely related species and its appreciation is of considerable evolutionary importance (Parsons 1973). In view of this, competition experiments have been made utilising taxonomically closely related species of the *immigrans* species group of the genus *Drosophila*. The parameters, namely their relative fitness and adaptedness, assessed in the present experiments are presented.

2. Materials and methods

For the present study, 6 species of the *immigrans* species group of *Drosophila* have been employed. They are *D. nasuta nasuta* (Coorg, Karnataka, India), *D.n. albomicana* (University of Texas, USA, collections 3045.11), *D. sulfurigaster neonasuta* (Coorg, Karnataka, India), *D.s. bilimbata* (University of Texas, USA, collections, 3071.6), *D. pulaua* (University of Texas, USA, collections 3121.5) and *D. hypocausta* (Coorg, Karnataka, India).

2.1 *Mixed cultures*

D. n. nasuta was made to compete separately with *D.s. neonasuta, D.s. bilimbata, D. pulaua* and *D. hypoucausta*; similarly, *D.s. neonasuta* was made to compete separately with *D.n. nasuta, D.n. albomicana* and *D. hypocausta.*

Each mixed culture was built with 12 females and 13 males of each species. Four

replicates were maintained for each mixed culture. The cultures were maintained at 21°C by the serial transfer technique of Ayala (1965). These mixed cultures were maintained till the elimination of one of the competing species.

The competitive fitnesses of the competing species were calculated by adopting the statistical procedure of Ayala (1969a). If the number of each species change at a constant rate, the fitness of one species relative to the other can be measured by two statistics m and W. The statistic m or logarithm relative fitness is estimated by the co-efficient regression of the natural logarithm of the ratio of the numbers of the two species on time (in weeks). The relative fitness, W, is the antilogarithm (to the base e) of m. If m_1 and m_2 measure the fitness of the two strains of one species or of two different species, the fitness of one relative to the other is given by $m_1 - m_2$. The method allows the measurement of both the fitness of one species relative to another and the fitness of strains of the same species relative to each other.

2.2 *Pure cultures*

For all the 6 species under study, single species populations were started with 25 pairs of flies. For each species 4 replicates were maintained at 21°C by adopting the serial transfer technique of Ayala (1965). These pure cultures were maintained for 30 weeks. The mean values for productivity and population size (two parameters of adaptedness) were calculated from 7th week onwards to the 30th week (24 counts).

3. Results and discussion

The interspecific competitive fitness of *D.n. nasuta* was measured during its competition with *D.s. neonasuta*, *D.s. bilimbata*, *D. pulaua* and *D. hypocausta*. In each of these mixed cultures, *D.n. nasuta* was found to eliminate its competitor. *D.s. bilimbata*, *D. pulaua* and *D. hypocausta* were eliminated rapidly within a period of 8 weeks. Particularly, *D.s. bilimbata* was eliminated within two weeks and hence it has not been considered for calculations. *D.s. neonasuta* was the only competitor to survive for a period of 28 weeks and was able to reproduce before it was eliminated by *D.n. nasuta*. The logarithm fitness m and the fitness, W, *of D.n. nasuta* relative to the other 3 species are given in table 1. The logarithm fitness is greater than zero and the relative fitness is more than one in all cases. Analysis of variance for the data in table 1 indicates significant heterogeneity among the 3 kinds of populations. A test for heterogeneity among replicates was made using as mean square error the mean variance of 16 populations. The replicates of the mixed culture *D.n. nasuta*/*D.s. neonasuta* are homogeneous, while others are heterogeneous. The fitness of *D.n. nasuta* with these 3 species, namely *D.s. neonasuta*, *D. pulaua* and *D. hypocausta*, relative to each other are given in table 2. *D.n. nasuta* has evinced maximum interspecific competitive fitness against *D. pulaua* and least against *D.s. neonasuta*.

Similarly, *D.s. neonasuta* was made to compete separately with *D.n. nasuta*, *D.n. albomicana* and *D. hypocausta*. *D.s. neonasuta* eliminates both *D.n. albomicana* and *D. hypocausta* but itself faces termination against *D.n. nasuta*. The logarithm fitness m and fitness, W, for the 12 populations of *D.s. neonasuta* are given in table 3. The analysis of variance for the data in table 3 indicates significant heterogeneity among the 3 kinds of populations. Replicates of *D.s. neonasuta*/ *D.n. albomicana* and *D.s. neonasuta*/*D.*

Table 1. Relative fitness (W) and logarithm relative fitness (m) of *D.n. nasuta* relative to *D.s. neonasuta*, *D. pulaua* and *D. hypocausta* in 12 experimental populations. The error and the variance of m are also given.

Populations	Species	$m \pm$ SE	Variance	W
1.	*D.n. nasuta/D.s. neonasuta*	0·0710 ± 0·020	0·0004	1·074
2.	"	0·0475 ± 0·017	0·0003	1·048
3.	"	0·0274 ± 0·020	0·0004	1·027
4.	"	0·0109 ± 0·020	0·0004	1·011
	Average	0·0392 ± 0·009	0·00009	1·040
5.	*D.n. nasuta/D. pulaua*	0·5556 ± 0·069	0·0048	1·743
6.	"	0·3921 ± 0·126	0·0159	1·480
7.	"	0·4277 ± 0·050	0·0025	1·534
8.	"	0·4584 ± 0·094	0·0089	1·581
	Average	0·4584 ± 0·045	0·0020	1·581
9.	*D.n. nasuta/D. hypocausta*	0·2400 ± 0·065	0·0042	1·272
10.	"	0·2576 ± 0·126	0·0158	1·293
11.	"	0·3256 ± 0·081	0·0066	1·385
12.	"	0·2340 ± 0·086	0·0074	1·264
	Average	0·2643 ± 0·046	0·0021	1·302

Table 2. Comparisons of fitness (W) and logarithm fitness (m) of *D.n. nasuta* as measured by the competition with *D.s. neonasuta*, *D. pulaua* and *D. hypocausta*.

Species	$m \pm$ SE	W	P
D.n. nasuta/D.s. neonasuta			
D.n. nasuta/D. pulaua	−0·4192 ± 0·032	0·6575	< 0·01
D.n. nasuta/D.s. neonasuta			
D.n. nasuta/D. hypocausta	−0·2251 ± 0·032	0·7984	< 0·01
D.n. nasuta/D. pulaua			
D.n. nasuta/D. hypocausta	+0·1941 ± 0·032	1·214	< 0·01

hypocausta are heterogeneous. The fitness of *D.s. neonasuta* with these 3 species, viz, *D.n. nasuta*, *D.n. albomicana* and *D. hypocausta*, relative to each other are given in table 4. The differences in fitness values between any two are strikingly significant, demonstrating that *D.s. neonasuta* has evinced different fitness values against its competitors. This indicates differences in the nature of competitive interactions in the mixed cultures of these species.

The intraspecific competitive fitness or the adaptedness of all 6 species is given in table 5. Adaptedness refers to the ability of the carriers of a genotype or a group of genotypes to survive and reproduce in a given environment (Dobzhansky 1968). Two related measures of adaptedness can be obtained, viz, 'productivity' and 'population size' in the experimental populations (Ayala 1965). This provides means for comparing the overall biological performance of one gene pool with another, where both are maintained under similar environmental conditions. Differences in productivity or population size between any two species under study are in most cases significant.

Table 3. Relative fitness (W) and logarithm relative fitness (m) of *D.s. neonasuta* relative to *D.n. nasuta*, *D.n. albomicana* and *D. hypocausta* in 12 experimental populations. The standard error and the variance of m are also given.

Populations	Species	$m \pm$ SE	Variance	W
13	*D.s. neonasuta/D.n. nasuta*	$-0{\cdot}0710 \pm 0{\cdot}020$	0·0004	0·9315
14	"	$-0{\cdot}0475 \pm 0{\cdot}017$	0·0003	0·9537
15	"	$-0{\cdot}0274 \pm 0{\cdot}020$	0·0004	0·9729
16	"	$-0{\cdot}0109 \pm 0{\cdot}020$	0·0004	0·9893
	Average	$-0{\cdot}0392 \pm 0{\cdot}009$	0·00009	0·9616
17	*D.s. neonasuta/D.n. albomicana*	$0{\cdot}2389 \pm 0{\cdot}157$	0·0248	1·270
18	"	$0{\cdot}0977 \pm 0{\cdot}079$	0·0063	1·103
19	"	$0{\cdot}0644 \pm 0{\cdot}046$	0·0021	1·066
20	"	$0{\cdot}0690 \pm 0{\cdot}040$	0·0016	1·071
	Average	$0{\cdot}1175 \pm 0{\cdot}046$	0·0021	1·123
21	*D.s. neonasuta/D. hypocausta*	$0{\cdot}5222 \pm 0{\cdot}162$	0·0264	1·686
22	"	$0{\cdot}4556 \pm 0{\cdot}082$	0·0068	1·573
23	"	$0{\cdot}3581 \pm 0{\cdot}079$	0·0062	1·431
24	"	$0{\cdot}3193 \pm 0{\cdot}046$	0·0021	1·376
	Average	$0{\cdot}4137 \pm 0{\cdot}051$	0·0026	1·512

Table 4. Comparisons of fitness (W) and relative fitness (m) of *D.s. neonasuta* as measured by the competition with *D.n. nasuta*, *D.n. albomicana* and *D. hypocausta*.

Species	$m \pm$ SE	W	P
D.s. neonasuta/D.n. nasuta			
D.s. neonasuta/D.n. albomicana	$-0{\cdot}1567 \pm 0{\cdot}058$	0·8553	$< 0{\cdot}01$
D.s. neonasuta/D.n. nasuta			
D.s. neonasuta/D. hypocausta	$-0{\cdot}4529 \pm 0{\cdot}058$	0·6357	$< 0{\cdot}01$
D.s. neonasuta/D.n. albomicana			
D.s. neonasuta/D. hypocausta	$-0{\cdot}2962 \pm 0{\cdot}058$	0·7437	$< 0{\cdot}01$

Thus, the differential ability of the species to exploit the experimental environment is striking. The comparisons of the parameters in the experimental populations can be summarized as follows: for productivity – *D.n. nasuta* > *D. hypocausta* > *D.s. neonasuta* = *D. pulaua* = *D.n. albomicana* = *D.s. bilimbata*; and for population size– *D.n. nasuta* > *D.s. neonasuta* > *D. hypocausta* > *D. pulaua* = *D.n. albomicana* = *D.s. bilimbata*. Essentially, the ability of a population to increase in numbers depends upon the birth rate and the survival rate of the animals. Those populations which have greater productivity have larger population size in the present experimental populations with the exception of *D. hypocausta*. Similar correlation between productivity and population size has been reported by Mourao *et al* (1972) in *D. willistoni* and Nirmala (1973) in *D. ananassae* and *D. melanogaster*.

Relevant literature reveals that there exist evidences both for correlation and lack of it, of the species performances in pure and mixed cultures. Tantawy and El-Wakil (1970) studied competition between *D. funebris* and *D. virilis* as well as fitness of these two species in isolation. On various fitness parameters, *D. funebris* was superior to *D. virilis* in isolation. However, in competition experiments, *D. funebris* was rapidly

Table 5. Mean values along with the standard errors of the productivity and population size in the population of 6 species.

Population	Species	Productivity	Population size
25	*D.n. nasuta*	70·00 ± 12·78	165·87 ± 16·35
26	"	71·20 ± 12·17	177·58 ± 18·93
27	"	67·91 ± 12·92	163·70 ± 21·66
28	"	85·75 ± 15·70	199·37 ± 24·04
	Average	73·71	176·63
29	*D.s. neonasuta*	52·54 ± 14·04	129·87 ± 16·33
30	"	46·20 ± 9·61	120·25 ± 18·08
31	"	42·00 ± 10·92	107·20 ± 17·11
32	"	40·54 ± 9·77	105·54 ± 14·81
	Average	45·32	116·71
33	*D.n. albomicana*	36·70 ± 7·85	74·04 ± 8·81
34	"	36·00 ± 7·91	68·79 ± 10·22
35	"	27·12 ± 5·35	56·95 ± 6·73
36	"	34·00 ± 7·76	70·20 ± 9·04
	Average	33·45	67·45
37	*D. pulaua*	45·25 ± 9·49	74·66 ± 12·13
38	"	34·95 ± 6·91	65·35 ± 8·88
39	"	32·83 ± 7·12	62·58 ± 8·15
40	"	37·79 ± 6·29	68·45 ± 8·43
	Average	35·20	67·76
41	*D.s. bilimbata*	32·75 ± 8·01	61·66 ± 7·75
42	"	31·66 ± 7·30	60·00 ± 8·32
43	"	36·54 ± 7·45	62·33 ± 8·52
44	"	35·33 ± 8·72	64·37 ± 8·93
	Average	34·07	62·09
45	*D. hypocausta*	32·71 ± 4·84	64·28 ± 6·06
46	"	56·14 ± 8·87	97·00 ± 12·88
47	"	68·57 ± 9·94	102·28 ± 13·87
48	"	72·57 ± 10·26	111·43 ± 16·27
	Average	57·49	93·74

eliminated. Barker and Podger (1970) found that *D. melanogaster* raised in mixed cultures were less fecund than those of pure cultures, while *D. simulans* showed reverse effect, in contrast to the reports of Ayala (1968, 1969b, 1970) and Nirmala (1973). They have demonstrated the existence of correspondence between adaptedness obtained from single species populations and those based on interspecies phenomena.

In the present experiments, *D.n. nasuta* out vies all the 4 species competitors namely, *D.s. neonasuta*, *D. hypocausta*, *D. pulaua* and *D.s. bilimbata*. These species are inferior to *D.n. nasuta* and hence there is a parallelism in the performances of these species in pure and mixed cultures. The relative fitnesses achieved by *D.n. nasuta* against these species differ significantly since it is an outcome of the competitive interaction of the two contesting species. Because of the least adaptedness of *D. pulaua*, *D.n. nasuta* was able to evince the highest fitness against it than against *D.s. neonasuta*, which has a better adaptedness than that of *D. pulaua*. *D.s. neonasuta* is a loser against *D.n. nasuta*, probably due to its lower adaptedness. Further, as *D.s. neonasuta* is superior to *D.n. albomicana* and *D. hypocausta*, it was able to supplant them in competition.

Thus, there exist evidences both for the negative and positive correlations between

inter- and intra-specific competitive fitnesses of species. Competitive ability is the sum total of numerous factors that interact exceedingly in complex ways. Therefore, under these circumstances it is difficult to predict the outcome of interspecies competition by judging the species performances in pure cultures. The single species (pure cultures) and two species (mixed cultures) populations represent models of two levels of complexity. Therefore, these laboratory populations can be utilized as biological models to study the dynamics and the process of competition.

These taxonomically closely related species of *Drosophila* under experimentation have reacted differently to the present experimental set up, each manifesting different levels of adaptedness and relative fitness. Thus, the present findings suggest the lack of correlation between taxonomic nearness and the ecological phenotype of *Drosophila* species under investigation.

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