Oecologia (1996) 108:72–78

Philip W. Hedrick · Elizabeth King

Genetics and the environment in interspecific competition: a study using the sibling species *Drosophila melanogaster* and *Drosophila simulans*

Received: 30 May 1995 / Accepted: 17 March 1996

Abstract The outcome of interspecific competition of two closely related species may depend upon genetic variation in the two species and the environment in which the experiment is carried out. Interspecific competition in the two sibling species, *Drosophila melanogaster* and *D. simulans*, is usually investigated using long-term laboratory stocks that often have mutant markers that distinguish them. To examine competition in flies that genetically more closely resemble flies in nature, we utilized freshly caught wildtype isofemale lines of the two species collected at the same site in San Carlos, Mexico. Under ordinary laboratory conditions, *D. melanogaster* always won in competition. However, in hotter and drier conditions, *D. simulans* competed much more effectively. In these environmental conditions, there were genetic differences in competitive ability among lines with the outcome of competition primarily dependent upon the line of *D. melanogaster* used but in some cases also influenced by the line of *D. simulans* used. Differences in the measures of productivity and developmental time did not explain the differences in competitive ability among lines. This suggests that the outcome of competition was not due to differences in major fitness components among the isofemale lines but to some other attribute(s) that influenced competitive ability. When lines of flies were combined, the outcome of competition was generally consistent with competitive outcomes between pairs of lines. In several cases, the combination of lines performed better than the best of the constituent lines, suggesting that competitive ability was combined heterotically and that the total amount of genetic variation was important in the outcome of interspecific competition.

Key words Competition · Environment · Fitness · Genetic variation · *Drosophila*

P. W. Hedrick (✉) · E. King
Department of Zoology,
Arizona State University,
Tempe, AZ 85287, USA

Introduction

The factors that allow two closely related species to coexist or that cause competitive exclusion of one of the two species has long been a fundamental question in population ecology and still remains so (e.g., Begon et al. 1990). In general, most attention has been paid to the environmental factors that influence coexistence or competitive exclusion. For example, the influence of various environmental parameters on the outcome of interspecific competition in two sibling species of flour beetles, *Tribolium castaneum* and *T. confusum* was examined in the classic work of Park and his colleagues (e.g., Neyman et al. 1958; Park 1964). In laboratory competition experiments of these two species, the outcome of competition was predictable under many environmental conditions, such as combinations of temperature and humidity, while in other environmental situations, the outcome appeared indeterminate.

In addition, it also has been long recognized that the genetic constitution of the competing species may influence the outcome of interspecific competition although the number of studies examining the role of genetic factors in interspecific competition are relatively few. For example, some strains of the two sibling species of *Tribolium* showed greater competitive ability than did others, illustrating the importance of genetic differences (Park et al. 1964). Similarly, Barker (1963) showed that the relative competitive ability of different laboratory strains of *Drosophila melanogaster* with its sibling species, *D. simulans*, varies dramatically. In addition, the competitive ability of a strain may change as in Hedrick (1973) who found that a mutant strain of *D. melanogaster* which lost in initial interspecific tests to *D. simulans* evolved over time so that it later won in interspecific competition tests.

D. simulans was first recognized by Sturtevant (1919) from strange female-only crosses in *D. melanogaster* as a sibling species of *D. melanogaster*, a species that had already been used for genetic research for over a decade. The two species are very similar in external morphology,

with virtually no differences in female morphology and only the genitalia of the males being quite different between the two species. In addition, the two species have strong genetic homology, with nearly identical chromosome banding patterns, and are generally quite close in their behavioral and ecological attributes. The two species coexist throughout much of the tropical and temperate regions of the world, but Dobzhansky and Pavan (1950) reported that *D. simulans* is generally more common in the tropics. In recent decades, *D. simulans* appears to be increasing in abundance (e.g., Hoenigsberg 1968; Tantawy et al. 1970) and also appears to have expanded its geographic range in many non-tropical areas. For example, *D. simulans* was first discovered in Japan in 1972 (Watanabe et al. 1984) and is now much more abundant than *D. melanogaster* in many areas of Japan (T. Yamazaki, personal communication). Of course, this apparent change in relative numbers may not be due only to interspecific competition but could also be influenced by the relative abundance of the resources and habitats used by the two species.

In many laboratory studies that use environmental conditions developed for *D. melanogaster, D. simulans* is quickly eliminated by interspecific competition. However, in the first study to examine the interspecific competitiveness of the two species, Sturtevant (1920) was able in some instances to keep the two species in mixed culture for as long as 5 months (around 10 generations). Generally, he found that *D. melanogaster* was the most common of the two species but that *D. simulans* became the relatively more abundant when the food became dry and old. Overall, *D. simulans* generally loses in laboratory competition so that most studies of interspecific competition of the two species have used mutant strains of *D. melanogaster* (and/or *D. simulans*), either to lower the competitive ability (or general fitness) of *D. melanogaster* and/or to allow identification of the two species without a microscope (e.g., Barker 1973; Futuyma 1970; Hedrick 1973). There is, therefore, a general paradox in that *D. simulans* is increasing in abundance and distribution in many parts of the world relative to *D. melanogaster*, including those that are not hot and dry, but generally it is not successful in laboratory experiments of interspecific competition with *D. melanogaster*.

In the following study, we utilize newly caught samples from natural populations at a single site, instead of long-term laboratory stocks which are generally marked by morphological mutants. This allows us to have samples that genetically more closely resemble those in natural populations rather than samples either adapted to laboratory conditions and/or with fitness that is influenced by mutant markers. The samples from nature were set up as isofemale lines, lines descended from only one female and, based on previous studies, either one, or at most several, males as parents of their progeny. Isofemale lines have been widely used to determine the extent of genetic variation for many quantitative traits in *Drosophila*. For example, if flies descended from different isofemale lines differ significantly for a quantitative trait when raised in a common environment, then this is strong evidence that there is genetic variation for the trait in the population being sampled (for details, see Hoffmann and Parsons 1988). Sampling the natural population to set up isofemale lines and the initial subsequent chance changes, primarily due to a combination of inbreeding and genetic drift, results in genetic differences between isofemale lines. Although most of these genetic differences probably do not strongly influence fitness, some of these chance changes may result in differential fitness among the isofemale lines.

In competition between individuals of the isofemale lines from the two species, we first determine the laboratory environmental conditions that allow *D. simulans* not to be quickly eliminated by *D. melanogaster*. We then characterize differences in competitive ability between isofemale lines of the two species. Finally, we examine the effect of combining lines of one or both species, which would increase the extent of genetic variation, on the outcome of interspecific competition. Because wild-type strains of the two species were used instead of ones with mutant morphological markers, the species composition was determined by examining the male genitalia under a binocular microscope. Overall, approximately 15,000 males were identified to species in this study.

Materials and methods

Strains of *Drosophila*

Over a 3-day period in March, 1993, T. Markow and P. Hedrick captured over fruit bait with an aspirator 59 female *Drosophila* (*melanogaster* or *simulans*) near a beach house in San Carlos, Sonora, Mexico. These female flies were brought back to Arizona State University and set up in individual vials to initiate 59 isofemale lines. By examining the emerging male progeny from each female, it was determined that 11 of the captured females were *D. melanogaster* and 48 were *D. simulans*, making only 18.6% of the females caught in this sample *D. melanogaster*. This suggests that *D. simulans* was the more common of the two species at this site and time.

Experiment 1

An initial experiment was set up to determine the interspecific competitive ability of these isofemale lines in normal laboratory conditions for *D. melanogaster*, i.e., temperature of 25 ± 0.5°C, humidity of 75 ± 5%, and 12-h light-dark cycle (this experiment was initiated as soon feasible after capture, i.e., after the progeny of the females were identified to species, the lines were stabilized in numbers, and flies to initiate the experiment were raised, starting on 28 May 1993). The flies were kept in half-pint milk bottles with cardboard tops. Eleven lines of *D. simulans* were randomly picked to compete with the 11 *D. melanogaster* lines. For each *D. melanogaster* – *D. simulans* combination, two replicates were set up, each with ten pairs of adult flies of each species so that the initial frequency of *D. simulans* was 0.5. On day 3, these adults were removed. On day 14, a sample of 50 random progeny males were examined under CO_2 anesthesia under a binocular microscope to determine the species composition. Overall, 1100 males were examined on day 14 of each generation of this experiment, near the maximum that could be confidently identified with good precision. All the progeny flies were then transferred to new bottles to be the adults for the next generation. This same procedure was carried out each generation.

Experiment 2

Of the above 11 combinations in experiment 1, 3 were chosen for further study in which *D. simulans* was in relatively high frequency at the end of the experiment, i.e., *D. melanogaster* 51 – *D. simulans* 56, *D. melanogaster* 55 – *D. simulans* 34, and *D. melanogaster* 57 – *D. simulans* 36, where the numbers refer to the specific isofemale lines (this experiment was initiated as soon as feasible after the completion of experiment 1, on 3 September 1993). All possible combinations of these three lines of each species competed against each other to determine if the effects were specific to particular combinations of the lines or were general to other lines. As the result of a pilot experiment (not reported here) to determine laboratory environmental conditions in which *D. simulans* competed better, the environment was changed to 27 ± 0.5°C and 35 ± 5% relative humidity, hotter and dryer than in experiment 1. In addition, different bottle tops were used made out of cloth material that allowed moisture to leave the bottle but still retained the flies. In the pilot experiment, we found that just changing the heat and humidity but leaving the top of the bottle the same as in experiment 1 appeared to result in little reduction in the internal humidity within the bottles. Otherwise, the techniques for this experiment were as given above for experiment 1.

Experiment 3

To determine the effect on competitive ability of a combination of several strains of a species, individuals from the three strains of a given species used in experiment 2 were combined and put in competition against a single strain (the same strains as in experiment 2) of the other species. This experiment was initiated as soon as feasible after the completion of experiment 2 (25 November 1993). For example, a mixture of five adult females of *D. melanogaster* from each of lines 51, 55, and 57 were used to initiate competition against 15 females from *D. simulans* line 56 so that the initial proportion of *D. simulans* was again 0.5. Using the three lines of each species from experiment 2, there were seven different combinations including the situation when all three lines are used for both species. This experiment was carried out under the same environmental conditions and in the same manner as experiment 2.

Productivity and developmental time

In the studies of Van Delden (1968), Hedrick (1973), and others, measures of components of fitness were consistent with the competitive ability observed in experiments with *D. melanogaster* and *D. simulans*. Therefore, we measured productivity, defined as the total number of progeny produced over 14 days, and developmental time, the time until adult emergence, for each of the three *D. melanogaster* and the three *D. simulans* lines used in experiments 2 and 3. Productivity is a composite measure of fitness and includes female fecundity and pre-adult survival.

For each line, 20 adult females were placed in half-pint milk bottles for 3 days at 27 ± 0.5°C and 35 ± 5% relative humidity. The progeny produced by these females were counted on days 10, 12, and 14. The total emergence for these 3 days is the productivity. Using the day-specific emergence times, developmental times were calculated assuming that the average fly emerged at the midpoint of the interval (the first interval was assumed to be day 8 to day 10).

Estimation of relative competitive ability

To determine the "average" competitive ability over all the generations in a given replicate of an experiment, we estimated the competitive ability of a particular *D. simulans* strain relative to a particular *D. melanogaster* strain in the following manner. The relative competitive ability for a particular replicate is defined as the value which gives the minimum squared deviation of the observed frequencies from the expected frequencies predicted. To calculate the expected proportions, it was assumed that the relative competitive ability of *D. simulans* was w and that of *D. melanogaster* was 1. Then, using the expression

$$p_{t+1} = \frac{p_t w}{p_t w + q_t} \quad (1)$$

where p_t and q_t are the frequencies of *D. simulans* and *D. melanogaster* in generation t, the expected proportions of the two species were calculated for each generation. This measure incorporates both the pattern and extent of change over the whole experiment and, therefore, gives a good measure of the average competitive ability over whole time course of the experiment.

Results

Experiment 1

In nearly all the combinations under the standard laboratory conditions for *D. melanogaster* used in experiment 1, the proportion of *D. simulans* declined with the average proportion of *D. simulans* after five generations being only 9.6% (Table 1). Note that this is in contrast to the frequency observed in nature where *D. simulans* constituted more than 80% of the sample. However, for several *D. melanogaster* – *D. simulans* combinations, i.e., lines 41–19, 51–56, 55–34, and 57–36, the frequency of *D. simulans* in one or both of the replicates was still substantial after five generations.

Table 1 The proportion of *D. simulans* out of 50 males over five generations in Experiment 1 when in competition with *D. melanogaster* for different pairs of isofemale lines at 25 C and 75% relative humidity. (– indicates no count made in this generation.)

D. m.	*D. s.*	Replicate	Generation				
			1	2	3	4	5
4	1	a	0.16	0.08	–	–	–
		b	0.30	0.42	0.44	0.12	0.02
7	9	a	0.08	0.02	–	–	–
		b	0.30	0.22	0.16	0.06	–
8	11	a	0.20	0.00	–	–	–
		b	0.32	0.04	–	–	–
30	13	a	0.20	0.28	0.22	0.04	–
		b	0.02	0.00	0.02	–	–
31	15	a	0.14	0.06	–	–	–
		b	0.24	0.26	0.06	–	–
41	19	a	0.20	0.20	0.28	0.02	–
		b	0.24	0.38	0.54	0.16	0.36
39	59	a	0.00	0.00	–	–	–
		b	0.26	0.16	0.00	–	–
51	56	a	0.36	0.50	0.54	0.34	0.50
		b	0.18	0.56	0.50	0.02	–
53	33	a	0.12	0.00	–	–	–
		b	0.08	0.04	–	–	–
55	34	a	0.50	0.20	0.28	0.10	0.06
		b	0.40	0.32	0.18	0.22	0.06
57	36	a	0.50	0.76	0.72	0.24	0.34
		b	0.64	0.64	0.92	0.48	0.76
Mean			0.248	0.234	0.221	0.082	0.096

Table 2 The proportion of *D. simulans* out of 50 males over ten generations in Experiment 2 when in competition with *D. melanogaster* for different pairs of isofemale lines at 27 C and 35% relative humidity. *w* is the competitive value of *D. simulans* relative to *D. melanogaster* (see text for details)

D. m.	*D. s.*	Replicate	Generation						
			1	2	3	4	7	10	*w*
51	34	a	0.42	0.36	0.62	0.42	0.36	0.14	0.894
		b	0.36	0.40	0.34	0.62	0.36	0.04	0.873
51	36	a	0.58	0.38	0.24	0.10	0.00	0.00	0.678
		b	0.68	0.28	0.26	0.28	0.28	0.12	0.819
51	56	a	0.48	0.44	0.34	0.40	0.26	0.08	0.841
		b	0.52	0.16	0.22	0.44	0.20	0.18	0.810
55	34	a	0.28	0.60	0.50	0.50	0.46	0.46	0.984
		b	0.34	0.70	0.32	0.60	0.46	0.28	0.948
55	36	a	0.24	0.42	0.22	0.52	0.06	0.06	0.783
		b	0.26	0.44	0.30	0.60	0.28	0.00	0.844
55	56	a	0.66	0.80	0.80	0.72	0.98	1.00	1.549
		b	0.46	0.66	0.80	0.80	0.98	1.00	1.455
57	34	a	0.60	0.70	0.54	0.84	1.00	1.00	1.398
		b	0.26	0.78	0.70	0.84	0.94	1.00	1.409
57	36	a	0.60	0.66	0.54	0.82	0.98	1.00	1.366
		b	0.46	0.46	0.56	0.80	1.00	1.00	1.307
57	56	a	0.36	0.78	0.74	0.82	0.80	0.84	1.304
		b	0.54	0.70	0.66	0.98	0.96	1.00	1.525
Mean			0.451	0.486	0.483	0.617	0.576	0.511	1.100

Experiment 2

In the hotter and drier environmental conditions of experiment 2, and using only lines in which *D. simulans* did relatively well in experiment 1, *D. simulans* competed much better than in experiment 1 (Table 2). After ten generations, the average proportion of *D. simulans* over the nine combinations was 0.511, slightly higher than the initial proportion of 0.5. However, four of the combinations resulted in the loss or near loss of *D. simulans*, all competition with *D. melanogaster* line 51 and the combination of *D. melanogaster* 55 and *D. simulans* 36. Four other combinations resulted in the loss or near loss of *D. melanogaster*, all combinations with *D. melanogaster* 57 and the combination of *D. melanogaster* 55 and *D. simulans* 56. The other combination, *D. melanogaster* 55 and *D. simulans* 34, still retained both species in both replicates in generation 10. In fact, these combinations were again counted in generation 16 and the proportion of *D. simulans* was 0.46 and 0.42 in replicates a and b, suggesting that the coexistence of these two species for these two lines was stable over approximately 8 months.

Note that the two replicates of each combination are generally quite similar, suggesting that the outcome of a particular competitive combination is governed by deterministic factors. Of course, some sampling variation is expected in the frequencies because a sample of 50 males was used to calculate the proportion in each generation.

Overall, the outcome of competition appears to be primarily determined by the line of *D. melanogaster* used, i.e., *D. melanogaster* 51 always won and *D. melanogaster* 57 always lost. The other line of *D. melanogaster*, 55, lost against *D. simulans* 56, had an apparent stable equilibrium with *D. simulans* 34 and won against *D. simulans* 36. On the other hand, each of the three *D. simulans* lines both won and lost in competition, depending upon the strain of *D. melanogaster*. There is also some variation in the competitive outcome due to line of *D. simulans* used when it is competed against *D. melanogaster* 55. In this case, *D. simulans* 36 loses in competition, *D. simulans* 34 appears to be in equilibrium, and *D. simulans* 56 wins, indicating that there is genetic variation for competitive ability among these three *D. simulans* lines.

The estimated relative competitive abilities for *D. simulans* are given at the extreme right-hand side of Table 2. If the value of *w* is greater than or less than unity, then it indicates that the relative competitive ability of *D. simulans* is greater than or less than, respectively, than that of *D. melanogaster*. For the four combinations in which *D. simulans* lost, these values ranged from 0.678 to 0.894 with a mean of 0.818. For the four combinations in which *D. simulans* won, the values ranged from 1.304 to 1.549 with a mean of 1.414. In the one combination in which there appeared to a stable equilibrium, the values for the two replicates were 0.948 and 0.984 with a mean of 0.966, very close to unity.

Experiment 3

In the first generation of experiment 3, the frequency of *D. simulans* was relatively low, with a mean of 0.334, in all these combinations (Table 3). The mean frequency over the ten generations of the experiment remained at about this level and was 0.283 in generation 10 even though *D. simulans* won in some of replicates. In all the combinations (and replicates) in which all three lines of *D. melanogaster* were used (four combinations each with two replicates) to start the experiment, *D. simulans* lost in competition. When all three lines of *D. simulans* were used to start the experiment, *D. simulans* won against *D.*

Table 3 The proportion over ten generations of *D. simulans* out of 50 males in Experiment 3 for competition between different isofemale lines, either one or a mixture of three, at 27 C and 35% relative humidity. *w* is the competitive value of *D. simulans* relative to *D. melanogaster* (see text for details)

D. m.	*D. s.*	Replicate	Generation						
			1	2	3	4	7	10	*w*
51, 55, 57	34	a	0.32	0.46	0.26	0.10	0.06	0.02	0.684
		b	0.52	0.46	0.32	0.16	0.04	0.00	0.731
51, 55, 57	36	a	0.44	0.28	0.30	0.04	0.00	0.00	0.632
		b	0.36	0.18	0.14	0.06	0.00	0.00	0.513
51, 55, 57	56	a	0.36	0.50	0.38	0.30	0.02	0.00	0.658
		b	0.06	0.24	0.06	0.14	0.00	0.00	0.307
51	34, 36, 56	a	0.18	0.26	0.34	0.38	0.30	0.34	0.883
		b	0.20	0.26	0.42	0.42	0.32	0.24	0.877
55	34, 36, 56	a	0.32	0.48	0.56	0.51	0.26	0.90	1.052
		b	0.34	0.24	0.18	0.26	0.28	0.46	0.880
57	34, 36, 56	a	0.44	0.54	0.30	0.64	0.94	0.98	1.204
		b	0.38	0.50	0.44	0.84	0.96	1.00	1.275
51, 55, 57	34, 36, 56	a	0.42	0.16	0.60	0.58	0.16	0.00	0.807
		b	0.34	0.40	0.38	0.56	0.26	0.02	0.847
Mean			0.334	0.371	0.303	0.361	0.257	0.283	0.811

melanogaster 57, appeared to be winning against one replicate of *D. melanogaster* 55, and the frequency in competition with *D. melanogaster* 51 remained at about the initial level.

Because *D. melanogaster* line 51 won against all three lines of *D. simulans* when by itself in experiment 2, the fact that it won when combined with the other *D. melanogaster* lines was to be expected. Similarly, because *D. melanogaster* 57 lost in competition with all the *D. simulans* lines, that it also lost when the three *D. simulans* lines were combined was also expected.

Some of the other results in this experiment were not as predictable. For example, *D. melanogaster* 55 lost to *D. simulans* 56 and won against *D. simulans* 36 in experiment 2. Here *D. melanogaster* 55 seemed to be losing to the combination of the three *D. simulans* lines in the first replicate and was near the frequency in generation 1 at the end of the experiment in the second replicate. In others words, in this case the combination of the three *D. simulans* lines appears to have not been as good as the highest of the three lines, *D. simulans* 56.

D. melanogaster 51, which beat all the *D. simulans* lines separately appeared to be at a stable level with the mixture. This is an example in which the combination of the three *D. simulans* lines did better than any of them did by themselves. Finally, the last combination in which all three lines from both species were used, *D. simulans* lost in both replicates. This suggests that the combination of the three *D. melanogaster* lines was better than just line 51, the best of the three lines, by itself.

Productivity and developmental time

The productivity of the three lines of the two species is given in Table 4. The overall mean for *D. simulans*, 486.8, is 42% higher than the mean for *D. melanogaster*, 342.3 ($P < 0.001$, nested ANOVA, SAS 6.09). Remember that in experiment 2, eight of the replicates were won by *D. simulans*, eight by *D. melanogaster*, and two still had both species coexisting, quite different from a prediction based on the higher mean productivity of *D. simulans*. If we look at the means for individual lines, there also seems to be little correspondence of productivity values and success in interspecific competition. For example, *D. melanogaster* 51 was the best interspecific competitor for the *D. melanogaster* lines but had the lowest productivity. Likewise, *D. simulans* 36 is the poorest of the *D. simulans* lines in interspecific competition, doing well only against *D. melanogaster* 57, but had the best productivity of the three *D. simulans* lines.

Table 4 The number of progeny produced over 14 days by 20 females of each of the three *D. melanogaster* and the three *D. simulans* used in experiments 2 and 3

Replicate	*D. melanogaster*			*D. simulans*		
	51	55	57	34	36	56
a	277	420	313	452	630	485
b	267	438	189	412	378	369
c	334	377	389	497	555	418
d	304	308	491	546	651	449
Mean	295.5	385.8	345.5	476.8	553.5	430.2

There was much less overall variation in the developmental time values, both within and between species (Table 5). The overall means for *D. simulans* and *D. melanogaster* were 10.28 days and 10.33 days, respectively, and were not statistically significantly different (nested ANOVA, SAS 6.09). Even the small, and statistically insignificant, differences in developmental times observed did not correspondence with measures of interspecific competitive ability. For example, *D. melanogaster* 51, which was the best interspecific competitor, had a longer than average developmental time (it is assumed that a shorter developmental time would be advantageous because early developing adults would have more resources available as larvae). Likewise, *D. simulans* 36, which

Table 5 The average developmental time (in days) for the three *D. melanogaster* and the three *D. simulans* lines used in experiments 2 and 3

Replicate	*D. melanogaster*			*D. simulans*		
	51	55	57	34	36	56
a	10.96	10.29	10.80	10.47	9.90	10.63
b	9.79	10.05	9.41	10.34	10.43	10.41
c	10.20	10.39	10.37	10.40	10.29	10.82
d	10.32	9.65	11.11	9.99	9.40	10.38
Mean	10.32	10.10	10.42	10.30	10.13	10.56

had relatively low interspecific competitive success, had the shortest developmental time of the *D. simulans* lines. The complete lack of correspondence of both these fitness components with interspecific competitive ability is somewhat surprising (see Discussion) because in other studies there has been an association (e.g., Hedrick 1973; Van Delden 1968).

Discussion

Various environmental factors appear to result in a predominance of one of two competing species in a particular area or in particular seasons. For example, for these two sibling species, *D. melanogaster* is much more abundant inside of wineries while *D. simulans* is more abundant outside of wineries (e.g., McKenzie 1974), corresponding to a higher tolerance to alcohol by *D. melanogaster* (McKenzie and Parsons 1972). In addition, seasonal differences in abundance occur so that *D. simulans* is much more abundant than *D. melanogaster* in certain seasons while the opposite occurs during other sampling periods (e.g., McKenzie and Parsons 1972; Rockwell et al. 1991; Watanabe et al. 1984). However, it has been somewhat perplexing to observe the nearly worldwide increase in *D. simulans* relative to *D. melanogaster* since *D. melanogaster* nearly always does better in interspecific laboratory competition.

Even though *D. simulans* was much more common (81.4%) than *D. melanogaster* in our sample from a natural population, under normal laboratory conditions *D. melanogaster* eliminated or nearly eliminated *D. simulans* in five generations in 18 out of initial 22 trials. In other laboratory conditions, higher temperature and lower humidity than normal laboratory conditions, the best of the wildtype *D. simulans* lines faired as well in competition as wildtype *D. melanogaster*. However, it is not clear how general these conditions are either spatially or temporally and perhaps some other component of the environment that is not mimicked in our laboratory conditions may be important in nature. The nearly equal outcome of the two species in interspecific competition of these selected lines was still not consistent with the much higher frequency of *D. simulans* in our wild caught sample.

In the present study, unlike almost all previous research on competition between the sibling species, *D. melanogaster* and *D. simulans*, we utilized newly caught samples from nature instead of longterm laboratory and/or mutant stocks. This allowed us to have samples that genetically more closely resembled those in nature rather than samples either adapted to laboratory conditions and/or with fitness that is influenced by mutant markers. We carried out our experiments as soon as feasible once the stocks were brought into the laboratory so that any differences that were observed could be attributed to genetic differences present in nature and not to differential adaptation to the laboratory environment. It is possible that some of the lines may have adapted to the laboratory environment more quickly that others (all were in the laboratory the same number of generations) so that this confounding effect may obscure some differences in the natural environment. However, in the experiment of Hedrick (1973) in which he found a reversal in competitive ability between *D. melanogaster* and *D. simulans*, the change took place over nearly two years rather than the short period in the laboratory in this study (see the description of the experiments for the exact dates of capture and the initiation of the experiments).

This study indicates that there is significant genetic variation in natural populations of both these species that is important in determining success in interspecific competition. For example, one line of *D. melanogaster* always won in competition while another line always lost. The third line of *D. melanogaster* won against one line of *D. simulans*, lost against another, and appeared to reach a stable equilibrium with the third. Further, genetic variation in *D. simulans* appeared to be important in determining the selective outcome in some instances.

In addition, our experiments demonstrated that a combination of lines can perform better than any of its constituent parental lines, suggesting that differences in competitive ability can be combined in a synergistic or heterotic manner. This increased competitive ability was apparent over ten generations so that it was not possible to determine whether it is the result of the sum of differences in additive effects, heterosis caused by dominance effects, or even some sort of epistatic change. Perhaps some of this effect is the result of cancelling out detrimental effects generated during the establishment of the isofemale lines although with the present experimental design, it is not possible to distinguish this possibility from additive or epistatic effects over lines. In one instance, however, the combination of the *D. simulans* lines did not exceed the best of the individual lines in competitive ability while it did in another comparison. Overall, it appears that the total amount of genetic variation is a very important factor in the interspecific competitive outcome of these two species.

We were not able to find a relationship with the measures of fitness that we examined and the interspecific competitive success. Surprisingly, the productivity of the *D. simulans* lines was much higher than the *D. melanogaster* lines, on the surface consistent with the higher frequency of *D. simulans* in the sampled population but not with the success of *D. melanogaster* in laboratory

competition. In a previous study (Hedrick 1973), a change in competitive ability of a *D. melanogaster* line was associated with changes in these fitness components. However, the present results indicate that the factors determining competitive success are not the major fitness components but perhaps other attributes that may play a significant role in determining competitive success. For example, pupation height in bottles may differ in these two species with *D. melanogaster* pupating higher on the side of the bottle and *D. simulans* often pupating in the media or lower on the side of the bottle (e.g., Barker 1971; Sokal et al. 1960; Van Delden 1968). In addition, other research have shown differences in these two species in oviposition site (Barker 1971; Soliman 1971), desiccation and heat resistance (Parsons 1983; Rockwell et al. 1991; Tantawy and Mallah 1961), and a variety of other attributes (e.g., Parsons 1983). Overall, it is not clear what is the mechanism of competition in these experiments and whether such factors as food limitation in adults leading to fecundity reduction, food limitation in larvae leading to lowered numbers of larvae, or other factors as mentioned above are important.

This study has demonstrated that both genetic and environmental factors can be of fundamental significance in determining the outcome of interspecific competition. The importance that we found of genetic variation in determining the outcome of interspecific competition illustrates the potential significance of genetic variation of interspecific competitive ability in different natural populations, particularly those founded with only a few individuals. In addition, potential rapid evolution of interspecific competitive ability (or the characteristics that influence it) in nature, either within a population or as the result of gene flow between populations is supported by the findings in this study.

Acknowledgements We appreciate the comments of Stuart Barker, Teri Markow, and Wilke Van Delden and several anonymous reviewers on the manuscript and thank Ruby Sheffer for carrying out the statistical analysis on the productivity and developmental time data.

References

Barker JSF (1963) The estimation of relative fitness of *Drosophila* populations. III. The fitness of certain strains of *Drosophila melanogaster*. Evolution 17: 138–146

Barker JSF (1971) Ecological differences and competitive interaction between *Drosophila melanogaster* and *Drosophila simulans* in small laboratory populations. Oecologia 8: 139–156

Barker JSF (1973) Natural selection for coexistence or competitive ability in laboratory populations of *Drosophila*. Egypt J Genet Cytol 2: 288–315

Begon M, Harper JL, Townsend CR (1990) Ecology, 2nd edn. Blackwell, Cambridge, Massachusetts

Dobzhansky T, Pavan C (1950) Local and seasonal variations in relative frequencies of species of *Drosophila* in Brazil. J Anim Ecol 19: 1–14

Futuyma D (1970) Variation in genetic response to interspecific competition in laboratory populations of *Drosophila*. Am Nat 104: 239–252

Hedrick PW (1973) Factors responsible for a change in interspecific competitive ability in *Drosophila*. Evolution 26: 513–522

Hoenigsberg HF (1968) An ecological situation which produced a change in the proportion of *Drosophila melanogaster* to *D. simulans*. Am Nat 102: 389–390

Hoffmann AA, Parsons, PA (1988) The analysis of quantitative variation in natural populations with isofemale lines. Genet Select Evol 20: 87–98

McKenzie JA (1974) The distribution of vineyard populations of *Drosophila melanogaster* and *Drosophila simulans* during vintage and non-vintage periods. Oecologia 15: 1–16

McKenzie JA, Parsons, PA (1972) Alcohol tolerance: an ecological parameter in the relative success of *Drosophila melanogaster* and *Drosophila simulans*. Oecologia 10: 373–388

Neyman J, Park T, Scott EL (1958) Struggle for existence; the *Tribolium* model: biological and statistical aspects. Gen Syst 3: 152–179

Park T (1964) Experimental studies of interspecies competition. II. Temperature, humidity, and competition in two species of *Tribolium*. Physiol Zool 27: 177–238

Park T, Mertz DB, Petrusewicz K (1964) Genetic strains and competition in populations of *Tribolium*. Physiol Zool 37: 97–162

Parsons PA (1983) The evolutionary biology of colonizing species. Cambridge University Press, Cambridge

Rockwell RF, Rosa de la ME, Guzman J, Laverde MJ, Levine L, Olvera O (1991) A temporal study of desiccation resistance of sibling *Drosophila* species from Laguna Verde, Veracruz, Mexico. Amer Midl Natur 126: 338–344

Soliman M (1971) Selection of site of oviposition by *Drosophila melanogaster* and *D. simulans*.Am Midl Nat 86: 487–493

Sokal RR, Ehrlich PR, Hunter PE, Schlager G (1960) Some factors affecting pupation site of *Drosophila*. Ann Entomol Soc Am 53: 174–182

Sturtevant, AH (1919) A new species closely resembling *Drosophila melanogaster*. Psyche 26: 153–155

Sturtevant, AH (1920) Genetic studies of *Drosophila simulans*. I. Introduction. Hybrids with *Drosophila melanogaster*. Genetics 5: 488–500

Tantawy AO, Mallah GS (1961) Studies on natural populations of *Drosophila*. I. Heat resistance and geographical variation in *Drosophila melanogaster* and *D. simulans*. Evolution 15: 1–14

Tantawy AO, Mourad AM, Masri A (1970) Studies on natural populations of *Drosophila*. VIII. A note on the directional changes over a long period of time in the structure of *Drosophila* near Alexandria, Egypt. Am Nat 104: 105–109

Van Delden W (1968) Fitness of experimental populations of *Drosophila melanogaster*, Ph. D. thesis, University of Groningen, Netherlands

Watanabe TK, Inoue Y, Watada M (1984) Adaptation of *Drosophila simulans* in Japan. Jpn J Genet 59: 225–235