RESEARCH ARTICLE

Variation in the relative magnitude of intraspecific and interspecific competitive effects in novel versus familiar environments in two *Drosophila* species

A M I T A B H J O S H I

Evolutionary Biology Laboratory, Evolutionary and Organismal Biology Unit,
Jawaharlal Nehru Centre for Advanced Scientific Research,
P. O. Box 6436, Jakkur, Bangalore 560 064, India

Abstract

Models of competitor coevolution, especially the genetic feedback hypothesis, suggest that a negative correlation between intraspecific and interspecific competitive effects may be important in sustaining competitor coexistence, and can give rise to oscillatory dynamics with repeated reversals of competitive superiority. I reanalyzed previously published census data from an experiment in which populations of *Drosophila melanogaster* and *D. simulans* underwent competitive coevolution in one familiar and two novel environments, to specifically look for any evidence of a negative relationship between intraspecific and interspecific competitive effects on population growth rates, and for any indication of short period cycling in the relative magnitude of intraspecific and interspecific competitive effects. While there was considerable variation in the relative magnitude of intraspecific and interspecific competitive effects over generations, among both populations and environments, there was no clear evidence supporting the genetic feedback hypothesis. Intraspecific and interspecific competitive effects on population growth rates were strongly positively correlated in novel environments, and uncorrelated in the familiar environment. Data from the familiar environment indicated that indices of competition of populations of the initially superior competitor, *D. melanogaster*, might be showing some cyclic behaviour, but I argue that this is likely to be transient, and not suggestive of sustained oscillatory dynamics predicted by the genetic feedback model. I discuss the results in the context of the importance of the genetic architecture of intraspecific and interspecific competitive abilities in determining the coevolutionary trajectory of competitive interactions.

Introduction

Competition between two species is a mutually antagonistic interaction with each species causing a reduction in either the population size (Barker 1971; Gurevitch *et al.* 1992) or rate of population growth (Levin 1971; Arthur 1987) of the other. Formal studies of competition as an ecological phenomenon go back to the early days of population ecology in the 1920s and 1930s (Kingsland 1995), but serious appraisal of intraspecific and interspecific competition as an evolutionary force began much later, in the 1960s (reviewed in Arthur 1982; Joshi *et al.* 2001). As discussed in detail by Arthur (1982), the principal focus of most early studies of interspecific competition as an evolutionary force was on the evolution of niche divergence via character displacement, character release, or both. Relatively fewer studies dealt with the possibility of evolutionary or coevolutionary increases in competitive ability per se (Arthur 1982), most likely because of the influence of the competitive exclusion principle and the paucity at the time of studies showing that coexistence of competitors was likely to be far more common than believed earlier (Joshi and Thompson 1995). Given the importance of interspecific competition in community structuring (MacArthur and Wilson 1967; Arthur 1987), the varied possible outcomes of competition (Arthur 1982), and the diversity of mechanisms that can promote competitor coexistence (Aarssen 1983; Tilman 1985; Begon and Wall 1987; Ellner 1987; Chesson 1990; Kishimoto 1990; Bengtsson 1991; Murray *et al.* 1992), it is clear that understanding the evolutionary

E-mail: ajoshi@jncasr.ac.in

consequences of interspecific competition is important to our understanding of how ecology and evolution interact to shape the living world.

The relative strength of interspecific versus intraspecific competitive effects, and their covariance, are central to analyses of the evolutionary consequences of interspecific competition (Bulmer 1974; Crozier 1974; Lawlor and Maynard Smith 1976; Levin and Udovic 1977; Slatkin 1980; Arthur 1986), especially with regard to the evolution or coevolution of competitive ability (Pimentel *et al.* 1965; Levin 1971; Léon 1974; Gill 1974; Pease 1984, 1985). Most theoretical treatments of the evolutionary consequences of interspecific competition referred to above are framed in the context of the Lotka-Volterra model of competition, which assumes linear density-dependence of realized per capita population growth rates, and can be expressed in two alternate forms, with different parameterization (Hastings 1997). In one case, the Lotka-Volterra model for two species can be described by two differential equations of the form

$$\frac{dN_i}{dt} = r_i N_i (1 - \alpha_{ii} N_i - \alpha_{ij} N_j) \qquad (1)$$

where N_i is the population size of the ith species, r_i is the maximal per capita growth rate of the ith species, and α_{ij} (i, $j = 1, 2$) measures the decrement in the realized per capita growth rate of the ith species as a consequence of adding one individual of the jth species. A more commonly used parameterization, originally due to Gause (1934), uses two differential equations of the form

$$\frac{dN_i}{dt} = \frac{r_i N_i}{K_i} (K_i - N_i - \alpha_{ij} N_j) \qquad (2)$$

where K_i is the equilibrium population size of the ith species in monoculture, and α_{ij} ($i \neq j$) measures the strength of the effect on the realized per capita growth rate of the ith species as a consequence of adding one individual of the jth species, relative to the effect on the realized per capita growth rate of adding one individual of the ith species. The interpretation of the interspecific competition coefficients α_{ij} ($i \neq j$), however, differs in the two versions of the model. In equation 2, α_{ij} reflects the magnitude of interspecific effects relative to intraspecific effects of the target species on itself, whereas α_{ij} in equation 1 is an absolute measure of the strength of interspecific competition. In equation 2, therefore, $\alpha_{ij} > 1$, $\alpha_{ij} = 1$, and $0 < \alpha_{ij} < 1$ represent, respectively, situations where an individual of species j inhibits the realized per capita growth rate of species i more than, equally, and less than an individual of species i itself. The corresponding conditions for equation 1, on the other hand, are $\alpha_{ij} > \alpha_{ii}$, $\alpha_{ij} = \alpha_{ii}$, and $\alpha_{ij} < \alpha_{ii}$, respectively.

Experimental studies on the laboratory evolution or coevolution of interspecific competitive ability have mostly been conducted on species of *Drosophila*, and several of these studies provide convincing evidence of evolutionary increases in some measure of competitive ability within at most a few tens of generations (Moore 1952; Ayala 1969a; Futuyma 1970; Arthur and Middlecote 1984; Mitchell and Arthur, 1991; Joshi and Thompson 1995, 1996). Explicitly interpreting the results from these experimental studies in light of the theoretical analyses of competitor coevolution in the Lotka-Volterra framework is, however, difficult for a number of reasons. In many of these studies, the focus was on the qualitative outcome of competition in terms of relative abundance of the competing species, and no attempts were made to actually estimate parameters such as competition coefficients. Estimating competition coefficients from such experiments is also not always a straightforward task (Ayala 1969b) and, moreover, there is evidence suggesting that *Drosophila* cultures in competition violate the linear density-dependence of per capita growth rates assumed by the Lotka-Volterra formulation (Ayala *et al.* 1973).

In any two-species competitive interaction, it is likely that there will be variation in the relative magnitude of intraspecific versus interspecific competitive effects on population growth rates. The theory suggests that, regardless of the underlying model of competition, such variation in the relative extent to which a species is inhibited by the presence of conspecific and heterospecific competitors, and whether intraspecific and interspecific competitive effects are correlated, can potentially affect the evolution of interspecific competitive abilities and, thereby, the evolutionary trajectory of the interaction (Pimentel *et al.* 1965; Levin 1971; Pease 1984). Moreover, the relative magnitude of intraspecific and interspecific effects may itself change over time as the competing species evolve. Yet, most experimental studies of competitive evolution do not report even crude estimates of the relative magnitude of intraspecific and interspecific competitive effects, their dynamic behaviour, or the relationship between them. Given that the 'true' model underlying competition between two species is likely to remain unknown, a start could be made by examining the time course of, and correlation between, crude empirical (model independent) measures of intraspecific and interspecific competitive effects in laboratory competition experiments.

In this paper, I present a new analysis of data from a previously reported study (Joshi and Thompson 1995, 1996) in which mixed cultures of *D. simulans* and *D. melanogaster* were maintained for eleven generations in three different one- and two-resource environments, along with single species cultures as controls. One of the one-resource environments had familiar food medium, the other a novel food medium, and the third was an environment in which the familiar and novel food media were available in equal quantities. The earlier published reports on this study focussed on two major sets of questions relating to interspecific competitive ability and its evolution in competing populations of two species that coexisted for eleven generations. First, whether competitive coevolution occurred during the course

of the experiment, and, if so, whether increased competitive ability was attained by increased effectiveness or tolerance or both (Joshi and Thompson 1995). Second, whether there was a correlation between competitive ability of a population of one species against the particular population of the other species with which it had been in competition for eleven generations, and its competitive ability against a naïve competitior population of the other species, and whether this correlation was stronger in novel rather than familiar environments (Joshi and Thompson 1996). In both these reports, the focus was on the outcome of the eleven generations of competition, and how it varied among replicate populations and environments. The results suggested that (a) competitive abilities did evolve in both species, through a variety of mechanisms, in the course of the experiment, (b) populations that were initially weaker competitors underwent relatively greater increases of competitive ability, and (c) evolutionary increases in competitive ability in the two novel environments were partly due to adaptation to the novel food medium. Here, I analyze the data from the experiment reported by Joshi and Thompson (1995, 1996) in order to assess the strength of intraspecific and interspecific competitive effects at each generation in the two species in the three environments, with particular emphasis on the relationship between these effects and their time course over the eleven generation experiment.

Materials and methods

As the results reported here are from a new analysis of a previously published data set, the complete details of the origins of the experimental populations and how the competition experiment was set up, as well as the rationale for the particular environmental conditions, can be found elsewhere (Joshi and Thompson 1995). Here, I provide a brief summary of the experimental design.

Experimental design

Three populations each of *D. simulans* (S-1, S-2, S-3) and D. melanogaster (M-1, M-2, M-3) were used in this study. The *D. melanogaster* populations were homozygous for the yellow body mutation, so that *D. melanogaster* flies could easily be distinguished from *D. simulans* flies during census. The experiment was conducted at 15°C, in a controlled environment chamber, under a 12:12 h light:dark cycle. Pairs of *D. melanogaster* and *D. simulans* populations (S-1, M-1; S-2, M-2; S-3, M-3) were kept in double-species cultures in three different environments for 11 generations. Single-species control cultures of each population in each of the three environments were also maintained for the duration of the experiment. All cultures were maintained in cages made up of two half-pint milk bottles, containing 45 ml of medium and a folded facial tissue, screwed into the base of a clear plastic box (15 cm × 9 cm × 4 cm) that connected

them. The three environments were cages containing two bottles of regular cornmeal-sugar-flour-agar medium (environment I), two bottles of regular medium with 4% ethanol (environment II), and one bottle each of regular medium and medium with 4% ethanol (environment I/II). Hence, a total of 18 single-species and 9 double-species cultures was set up. Each generation, 50 males and 50 females of each species in the double-species cultures (100 males and 100 females in the single-species cultures) were allowed to lay eggs for 3 days in a cage and were then discarded, thereby maintaining constant total density of 200 breeding adults in all cultures. For each species, adult offspring were censused on the 45th day after the commencement of egg laying, and the required number of males and females chosen in an unbiased manner to initiate the next generation. Environment I was a familiar environment for these populations, as they had been kept on corn meal food for many generations prior to the assay. Corn meal food with 4% ethanol constituted a novel food medium for the two species, and, moreover, a deleterious one with relatively greater harmful effects on *D. simulans* (Joshi and Thompson 1995).

Calculation of indices of competition

The index of competition for each species in a given environment was defined as the decrement in the per capita population growth rate — at a total breeding density of 200 flies per culture, regardless of species — of the target species caused by the presence of the other species. The indices of competition for *D. melanogaster* (C_M) and *D. simulans* (C_S), in each of the three environments, were, therefore, calculated each generation as

$$C_M = \frac{N_{Sa}}{n_{Sa}} - \frac{N_{Sc}}{n_{Sc}} \qquad (3)$$

$$C_S = \frac{N_{Ma}}{n_{Ma}} - \frac{N_{Mc}}{n_{Mc}} \qquad (4)$$

where N is the number of eclosing adults in a given generation, and n the number of adults comprising the breeding population in the previous generation. The subscripts *a, c, S,* and *M* refer to single-species cultures (alone), double-species cultures (competition), *D. simulans*, and *D. melanogaster,* respectively. Each of the three replicate sets of six single-species and three double-species cultures was, thus, treated as a block for analysis; the rationale for this has been described by Joshi and Thompson (1995). In the experiment, n_{Sa} and n_{Ma} were fixed at 200 individuals, and n_{Sc} and n_{Mc} were fixed at 100 individuals in every generation. N_{Sa}, N_{Sc}, N_{Ma} and N_{Mc} were obtained each generation from the census data, and have been previously reported by Joshi and Thompson (1995, figure 2).

Negative, zero and positive indices of competition of a

Table 1. Summary of results from two separate mixed model analyses of variance (ANOVA) carried out on the mean index of competition and the mean absolute one-step fluctuation in the index of competition (averaged over 11 and 10 generations, respectively) in the two species in mixed cultures in the three environments. In this model, effects including the random factor (block) cannot be tested for significance and have, therefore, been omitted for brevity.

Effect (d.f. 1,2)	Mean C		Mean fluctuation in C	
	F	P	F	P
Environment (2,4)	1.69	0.293	44.85	0.002
Species (1,2)	104.16	0.009	11.60	0.076
Environment × Species (2,4)	6.49	0.055	16.39	0.012

species imply that its inhibitory effect on the per capita population growth rate of the other species is, respectively, less than, equal to, or greater than the intraspecific inhibitory effect that individuals of the second species exert on their own per capita population growth rate, at least at this fixed breeding adult density. It can be argued that the density of each individual species in the double-species cultures is effectively half of that in the corresponding single-species cultures, because there are only half as many breeding adults of that species in a double-species culture. Given the close similarity in the laboratory ecology of *D. simulans* and *D. melanogaster* (Parsons 1975), this is unlikely to have a major effect on the strength of intraspecific competition in single- versus double-species cultures, as compared to the effect of total density of both species. Since both species-specific and overall densities could not be simultaneously equalized in the experiment, the latter were equalized (Joshi and Thompson 1995). These indices of competition, thus, empirically measure the relative magnitude of interspecific competitive effects of each species on the other, relative to the intraspecific competitive effect the target species has on its own per capita growth rate. The indices of competition are, therefore, crudely analogous to competition coefficients in the canonical form of the Lotka-Volterra model for two-species competition (equation 2), although unlike the Lotka-Volterra competition coefficients, the indices of competition are not based on any specific underlying model of population growth.

Statistical analysis

All analyses were implemented on STATISTICA™ for Windows Release 5.0 B (StatSoft Inc. 1995). The correlation between per capita growth rates, at a total breeding density of 200 adults per culture, in single- or double-species cultures was estimated for each species × environment × repli-

cate population combination. All other analyses used the indices of competition at every generation for each population of *D. simulans* and *D. melanogaster* in mixed culture (C_S and C_M, respectively) as input data. Mean C values for each species × environment × replicate population combination, averaged over the 11 generations of the experiment, were subjected to mixed model analysis of variance (ANOVA) treating block (replicate) as a random factor, and environment and species as fixed factors crossed with block and one another. A similar ANOVA was carried out on mean absolute value of the one-step fluctuation of C values for each species × environment × replicate population combination, estimated as

.

$$\text{mean one-step fluctuation} = \frac{1}{10} \sum_{t=1}^{10} \left| C_{i(t+1)} - C_{i(t)} \right|, \quad (5)$$

where $i = S, M$

Multiple comparisons were done using Tukey's HSD test. The C values for each species × environment × replicate population combination were also subjected to time-series analysis, including the estimation of autocorrelations, periodograms, and the cross correlation between C_M and C_S at different lags. For the spectral analysis yielding the periodograms, only data from generations 2-11 were used to keep the number of terms in the time series even.

Results

Per capita growth rates in both single-species ($N_{ia}/200$; $i = S, M$) and double-species ($N_{ic}/100$; $i = S, M$) cultures, in general, tended to be higher in *D. melanogaster* than in *D. simulans,* especially in the novel environments II and I/II (data not shown). In most replicates of both species, per capita growth rates in single- and double-species cultures were strongly significantly positively correlated ($r > +0.90$,
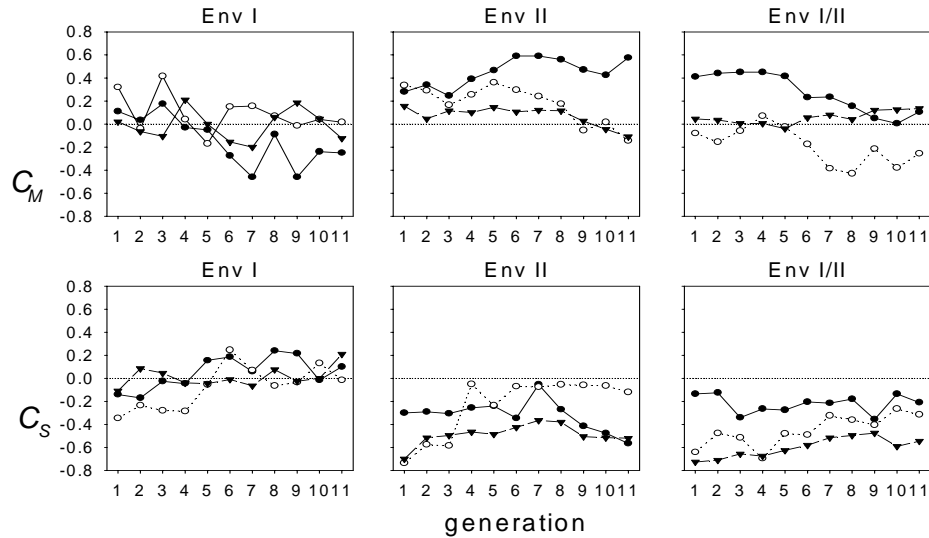
Figure 1. Indices of competition for the three populations each of *D. melanogaster* (C_M) and *D. simulans* (C_S) in the three environments (filled circles: block 1; open circles: block 2; filled triangles: block 3).

$P < 0.001$ in S-1, S-2, S-3, M-1 and M-3 in environments II and I/II). Replicate M-2 of *D. melanogaster* was the sole exception to this pattern, showing no significant correlation between per capita growth rates in single-species ($r > +0.36$, $P = 0.27$) and double-species ($r > +0.38$, P = 0.25) cultures. In the familiar environment I, however, there was no significant correlation between per capita growth rates in single- and double-species cultures of either species (-0.08 < r < +0.48, $P > 0.14$ in all replicates).

In both species, considerable variation was observed in the pattern of change of indices of competition over time among environments, as well as among replicate populations in the same environment, especially in the novel environments II and I/II (figure 1). Overall, the trend was for C_S to increase over time, especially in environments I and I/II (figure 1), which is consistent with earlier observations on measures of competitive ability in this experiment (Joshi and Thompson 1995). The ANOVA on mean C revealed a significant main effect of species (mean C_M > mean C_S), largely due to the difference between species in the novel environments II and I/II, reflected also in the near significant environment × species interaction (table 1). The degree of generation to generation fluctuation in C values was significantly greater for both species in the familiar environment I, rather than in the two novel environments II and I/II, whereas the mean absolute value of the one-step fluctuation of C_M values was significantly greater than the mean for C_S values only in the familiar environment I, a pattern of results reflected in the ANOVA as well (table 1).

The autocorrelation and spectral analyses did not reveal any clear and consistent evidence for relatively short-period cycles in the indices of competition C_S and C_M (figures 2, 3, 4; table 2). However, some rough trends are discernible. Both species in the one-resource novel environment II show the least indications of any fine structuring to the dynamics of C values over time (figure 3; table 2), except for overall trends, as can be seen in figure 1. In environment II, over 50% of the contribution to the periodogram in both species is due to period 10, analogous to residual error (table 2). There is no indication of a prominent peak in periodogram values due to any of the shorter periods (table 2). Similarly, the autocorrelations for both species in environment II reveal a weak pattern of positive correlations (not always significant) at small lags, tapering off into zero, or weakly negative correlations as the lag increases (figure 3). This is likely to be a reflection of the fact that C values for populations of the two species in environment II tend to fall relatively evenly into two bands, one slightly higher than the other, with values in the higher band showing a run of 6-7 generations (figure 1).

The populations in the familiar environment I show stronger evidence of some structure to the variation over time in C values; some difference between species, and among replicate populations of a species, is also apparent (figure 2). In the case of *D. melanogaster*, especially in replicates M-2 and M-3, there is evidence for a large contribution of period 3.33 and 5.0 oscillations, respectively, to the pattern of fluctuation, accompanied by a very low contribution of period 10 (table 2). The autocorrelations for replicates M-2 and M-3 also reflect a contribution of relatively short period oscillations in the negative correlations present at low lags (figure 2). However, replicate M-1 has a relatively large (31%) contribution of period 10 to the periodogram, and the autocorrelation pattern, too, is suggestive of either no clear single periodicity or, at best, a somewhat longer term periodicity. Although the periodogram

Table 2. Results of spectral analysis on the indices of competition for the two species in mixed cultures. Entries are the fractional contributions of each period to the periodogram.

	Period				
	2.0	2.5	3.33	5.0	10
Environment I					
M-1	0.04	0.51	0.09	0.05	0.31
M-2	0.03	0.23	0.51	0.23	0.03
M-3	0.13	0.06	0.05	0.75	0.01
S-1	0.06	0.16	0.21	0.04	0.53
S-2	0.09	0.01	0.21	0.35	0.34
S-3	0.01	0.19	0.14	0.21	0.45
Environment II					
M-1	0.02	0.06	0.09	0.26	0.57
M-2	0.12	0.10	0.04	0.09	0.65
M-3	0.02	0.05	0.01	0.08	0.84
S-1	0.05	0.16	0.12	0.10	0.57
S-2	0.23	0.13	0.07	0.09	0.48
S-3	0.03	0.01	0.08	0.20	0.68
Environment I/II					
M-1	0.30	0.03	0.44	0.04	0.19
M-2	0.13	0.19	0.01	0.45	0.22
M-3	.03	0.26	0.24	0.17	0.30
S-1	063	0.08	0.03	0.23	0.03
S-2	0.03	0.45	0.04	0.36	0.12
S-3	0.15	0.02	0.06	0.27	0.50

Since the time series was only 10 generations long, the contribution of period 10 is analogous to a residual error term.

for replicate M-1 in environment I shows a peak at period 2.5 (table 2), this is actually due to large cosine and sine coefficients of opposing sign (data not shown) and this is the likely explanation of why the autocorrelation does not reveal clear signs of a 2-3 generation cycle in C_M (figure 2). In the case of *D. simulans* in environment I, there is a large contribution of period 10 in all three replicates, and no distinct large peaks at any one period less than 10 in the periodogram (table 2). The autocorrelation patterns for *D. simulans* are quite variable, with the pattern for replicate S-1 being similar to that of M-1, whereas there are mostly small correlations at the various lags in replicates S-2 and S-3 (figure 2).

The results of time series analyses on the *D. melanogaster*

and *D. simulans* populations in the two-resource environment I/II are somewhat intermediate between those from environments I and II (figure 4; table 2). The autocorrelation pattern for all three replicates of *D. melanogaster* is strong and consistent: significant and decreasing positive correlations for lags 1 and 2, giving way to increasingly negative correlations by lag 5 or 6 (figure 4), suggestive of *C* values tending to fall relatively evenly into two bands, one slightly higher than the other, with values in the higher band showing a run of 6-7 generations. The autocorrelations for *D. simulans* replicates S-2 and S-3 in environment I/II follow a pattern similar to that of *D. melanogaster,* whereas replicate S-1 shows a pattern consistent with weak small period cycles (figure 4). The periodograms show a moderate to
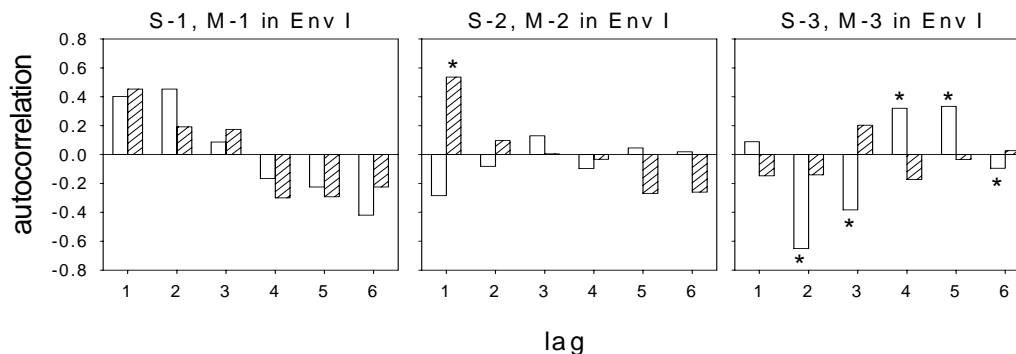
Figure 2. Autocorrelation coefficients for the indices of competition for the three populations each of *D. melanogaster* and *D. simulans* in environment I (open bars: C_M; hatched bars: C_S; *: *P* < 0.05).

Table 3. Cross-correlations between indices of competition for the two species in mixed cultures. Entries are the correlation coefficients (r) between C_M at generation t and C_S at generation $t + lag$.

	lag				
	-2	-1	0	+1	+2
Environment I					
S-1, M-1	-0.56	-0.89[**]	-0.58[*]	-0.43	-0.47
S-2, M-2	-0.27	+0.17	-0.30	-0.66[**]	-0.31
S-3, M-3	+0.48	+0.31	-0.26	-0.03	+0.40
Pooled	-0.44[**]	-0.39[**]	-0.49[**]	-0.54[**]	-0.37[*]
Environment II					
S-1, M-1	-0.08	+0.07	-0.01	+0.07	-0.32
S-2, M-2	-0.51	-0.40	-0.40	-0.41	-0.16
S-3, M-3	-0.31	+0.24	+0.08	+0.43	+0.28
Pooled	+0.07	+0.12	+0.06	+0.10	+0.09
Environment I/II					
S-1, M-1	+0.21	+0.13	-0.07	-0.24	-0.35
S-2, M-2	-0.35	-0.57[*]	-0.87[**]	-0.57[*]	-0.40
S-3, M-3	+0.84[**]	+0.72[**]	+0.54[*]	+0.32	+0.19
Pooled	+0.39[**]	+0.34[*]	+0.27	+0.29	+0.35[*]

** $P < 0.05$

* $0.05 < P < 0.10$

Pooled correlation coefficients estimated using data from all three blocks within an environment.

high contribution of period 10 in all populations except replicate S-1, which also shows a distinct and large peak at period 2 (table 2). None of the other five populations have a single large peak at periods less than 10 (table 2).

The cross-correlation analysis shows that, at least in the novel environment II, C_S and C_M tend to be uncorrelated with one another, either in the same generation, or up to two generations before or after (table 3). In the familiar environment I, C_S and C_M in individual replicates are either significantly negatively correlated or uncorrelated at lags -2 to +2 (table 3), indicating that over spans of a few generations, indices of competition for the two species tend to vary inversely, as can also be seen from figure 1. Once again, the results for the two-resource environment I/II are somewhere between those for environments I and II. Cross-correlation patterns in individual replicates vary considerably, ranging from no significant correlations at any lag from -2 to +2, to mostly negative or mostly positive correlations at various lags (table 3).

Discussion

The per capita growth rates in single- and double-species cultures, estimated for a breeding density of 200 adults regardless of species, provide a crude measure of the strengths of intraspecific and interspecific competition, respectively. The observation that these measures are positively correlated in most populations in the novel environments, and uncorrelated in the familiar environment, agrees with the earlier result that evolution of competitive ability in the novel environments is, in part, due to adaptation to the novel (and somewhat toxic) ethanol containing food medium (Joshi and

Thompson 1996). The lack of a negative correlation between the strength of intraspecific and interspecific competition — even in the familiar environment where competitive ability is much more dependent on adapting to the competitor population (Joshi and Thompson 1996) — suggests that the condition of an antagonistic relationship between the strength of intraspecific and interspecific competition required by some models of evolutionary reversals of competitive superiority (Pimentel *et al.* 1965; Levin 1971; Pease 1984) may not often be met in species that are ecologically very similar.

The observed overall trend of evolutionary increase in the index of competition of *D. simulans* (C_S), while that of *D. melanogaster* (C_M) remains constant or decreases (figures 1), is consistent with the asymmetric evolution of competitive ability, measured though effects on population size, observed in these experimental populations (Joshi and Thompson 1995). Indeed, the index of competition used in this study is very similar to the measure of competitive effectiveness used by Joshi and Thompson (1995), differing only in the scaling terms. As a heuristic measure of the relative magnitude of interspecific effects of one species on the other, compared to the effects of the target species on its own growth rate, however, the index of competition is easier to interpret than competitive effectiveness, as it is symmetric around zero. The magnitude of fluctuations in indices of competition being greater in the familiar environment than in the novel environments (figure 1) is also consistent with the earlier finding that adaptation to the novel food medium is an important component of increased competitive ability in the novel environments (Joshi and Thompson 1995). On
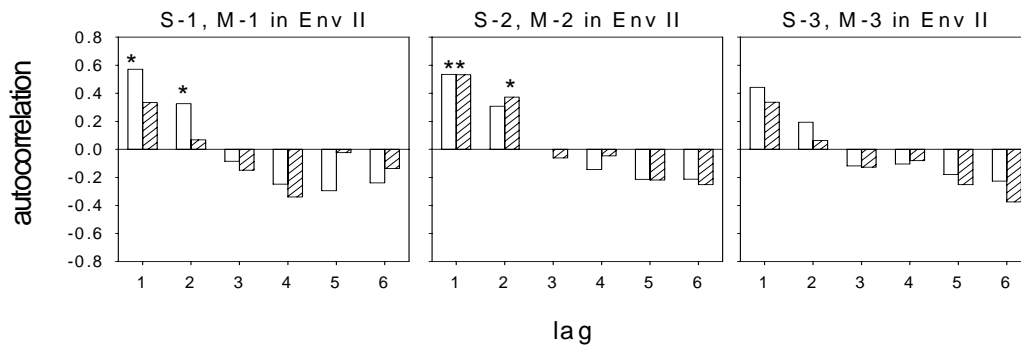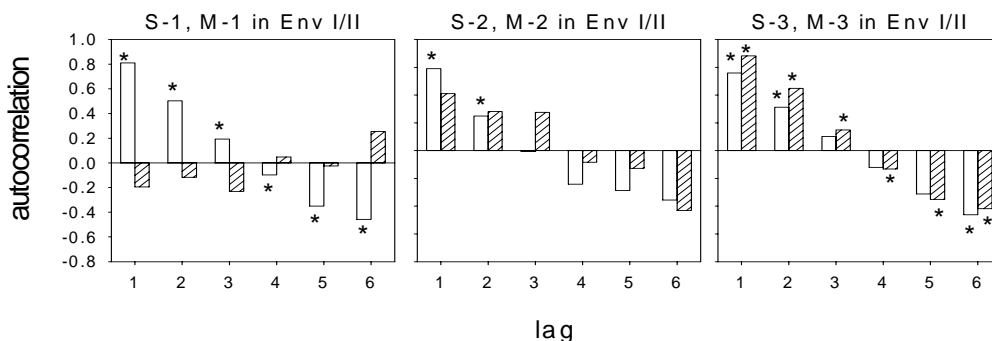
Figure 3. Autocorrelation coefficients for the indices of competition for the three populations each of *D. melanogaster* and *D. simulans* in environment II (open bars: C_M; hatched bars: C_S; *: $P < 0.05$).

average, C_M values fluctuated more than C_S values from one generation to the next only in the familiar environment I (figure 1); the implication of this observation is not clear at this time, although it is tempting to speculate that it is somehow related to *D. melanogaster* initially being the stronger competitor, resulting in greater evolution of competitive ability in *D. simulans* (Joshi and Thompson 1996).

The results of the time series analyses on the indices of competition, taken together, do not provide any strong evidence for short period (few generation) cycles in relative magnitudes of intraspecific and interspecific competition (figures 2, 3, 4; table 2), such as would be expected under the genetic feedback hypothesis of Pimentel *et al.* (1965). Of course, the spectral analysis does provide some evidence for possible cyclic dynamics of C_M (table 2) in the period range of 2.5 – 5.0 generations, but in the absence of a negative correlation between intraspecific and interspecific competitive effects it is difficult to relate the possible cycling of C_M to the competitive interaction with *D. simulans.* The cross-correlations between C_M and C_S also do not provide any evidence for short period cycling or an antagonistic relationship between intraspecific and interspeficic competitive effects (table 3); were the latter the case, then signs of cross-correlations would be expected to change with lag, at least once in five generations.

In general, all analyses point towards the time-structuring of the dynamics of *C* values being different in the familiar

environment versus the two novel environments, and differing between *D. melanogaster* and *D. simulans* only in the familiar environment. Because the *C* values reflect the effect of one species on the per capita growth rate of the other, relative to the effect of that species on its own growth rate, a negative C_i implies that the growth rate of target species *j* is negatively affected by conspecific individuals to a greater degree than it is by individuals of the other species *i*. This can also be interpreted as suggesting that the target species *j* is under greater selection for increased intraspecific competitive ability, whereas the other species *i* is under greater selection for increased interspecific competitive ability, especially in this study where the numbers of breeding adults of both species are equalized each generation. From this viewpoint, populations of *D. melanogaster* in the two novel environments are under stronger selection for increased intraspecific rather than interspecific competitive ability, as $C_S < 0$ in all three replicates in environments II and I/II (figure 1). Of course, these *D. melanogaster* populations are also under selection to adapt to the ethanol containing food medium (Joshi and Thompson 1996). Given the strong positive correlation between per capita growth rates in single- and double-species cultures in these environments, adaptation to ethanol would tend to increase both intraspecific and interspecific competitive ability. In the familiar environment, the relative strength of selection on intraspecific versus interspecific competitive ability in both

Figure 4. Autocorrelation coefficients for the indices of competition for the three populations each of *D. melanogaster* and *D. simulans* in environment I/II (open bars: C_M; hatched bars: C_S; *: $P < 0.05$).

species probably reverses over the course of the experiment (figure 1), as *D. simulans* populations evolve greater competitive ability, part of which is specific to the particular competitor population *D. melanogaster* (Joshi and Thompson 1996). However, given that per capita growth rates in single- and double-species cultures in environment I are uncorrelated, and that C_S and C_M values appear to be converging onto a band close to zero towards the end of the experiment, this reversal is more likely to have led to stable coexistence if the experiment had been continued for more generations, rather than oscillatory dynamics as predicted by the genetic feedback model (Pimentel *et al.* 1965). The present results, thus, support the view that the conditions for repeated reversals of competitive ability may not often be seen in real populations (Levin 1971; Arthur 1982). Indeed, there appears to be only one study that yielded evidence for an inverse relationship between intraspecific and interspecific competitive ability in three wild-type strains of *D. willistoni*, when competed with a mutant conspecific strain, and with *D. nebulosa* (Levin 1969).

Ultimately, assessing the genetic rather than phenotypic correlation between intraspecific and interspecific competitive ability in different populations is what is required to understand the effect of changes in the nature of a competitive interaction on its evolution (Pease 1984), but that is an extremely daunting task. Moreover, genetic correlations are liable to change over the course of selection even in a few tens of generations (Chippindale *et al.* 2003). If the genetic correlation between intraspecific and interspecific competitive ability is itself likely to evolve in competing populations, it would introduce a further level of variation affecting the coevolution of competitors. Variation among populations and environments in the genetic architecture of intraspecific and interspecific competitive effects could promote variation in the evolutionary outcome of competition in different populations over a geographic range. Such variation in outcomes, along with processes of extinction and migration, can substantially affect the evolution of interactions between geographically structured species (Thompson 1994). To better understand how variation in selection pressures generated by competition affects the evolution of competitive interactions, an understanding of the genetic relationship between intraspecific and interspecific competitive abilities in various species is of critical importance.

References

Aarssen L. W. 1983 Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. *Am. Nat.* **122**, 707–731.

Arthur W. 1982 The evolutionary consequences of interspecific competition. *Adv. Ecol. Res.* **12**, 127–187.

Arthur W. 1986 On the complexity of a simple environment: competition, resource partitioning and facilitation in a two-species *Drosophila* system. *Phil. Trans. R. Soc. London.* B **313**, 471–508.

Arthur W. and Middlecote J. 1984 Evolution of pupation site and interspecific competitive ability in *Drosophila hydei. Biol. J. Linn. Soc.* **23**, 343–352.

Arthur W. 1987 *The niche in competition and evolution.* Wiley, Chichester.

Ayala F. J. 1969a Evolution of fitness. IV. Genetic evolution of interspecific competitive ability in *Drosophila. Genetics* **61**, 737–747.

Ayala F. J. 1969b Experimental invalidation of the principle of competitive exclusion. *Nature* **224**, 1076–1079.

Ayala F. J., Gilpin M. E. and Ehrenfeld J. G. 1973 Competition between species: theoretical models and experimental tests. *Theor. Pop. Biol.* **4**, 331–356.

Barker J. S. F. 1971 Ecological differences and competitive interaction between *D. melanogaster* and *D. simulans* in small laboratory populations. *Oecologia* **8**, 139–156.

Begon M. and Wall R. 1987 Individual variation and competitor coexistence: a model. *Func. Ecol.* **1**, 237–241.

Bengtsson J. 1991 Interspecific competition in metapopulations. *Biol. J. Linn. Soc.* **42**, 219–237.

Bulmer M. G. 1974 Density-dependent selection and character displacement. *Am. Nat.* **108**, 45–58.

Chesson P. L. 1990 Geometry, heterogeneity and competition in variable environments. *Phil. Trans. R. Soc. London.* B **330**, 165–173.

Chippindale A. K., Ngo A. L. and Rose M. R. 2003 The devil in the details of life-history evolution: instability and reversal of genetic correlations during selection on *Drosophila* development. *J. Genet.* **82**, 133–145.

Crozier R. H. 1974 Niche shape and genetic aspects of character displacement. *Am. Zool.* **14**, 1151–1157.

Ellner S. P. 1987 Alternate plant life-history strategies and coexistence in randomly varying environments. *Vegetatio* **69**, 119–208.

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

Gause G. F. 1934 *The struggle for existence.* Williams and Wilkins, Baltimore.

Gill D. E. 1974 Intrinsic rates of increase, saturation densities, and competitive ability. II. The evolution of competitive ability. *Am. Nat.* **108**, 103–116.

Gurevitch J., Morrow L. L., Wallace A. and Walsh J. S. 1992 A meta-analysis of competition in field experiments. *Am. Nat.* **140**, 539–572.

Hastings A. 1997 *Population biology: concepts and models.* Springer, New York.

Joshi A. and Thompson J. N. 1995 Alternative routes to the evolution of competitive ability in two competing species of *Drosophila. Evolution* **49**, 616–625.

Joshi A. and Thompson J. N. 1996 Evolution of broad and specific competitive ability in novel versus familiar environments in *Drosophila* species. *Evolution* **50**, 188–194.

Joshi A., Prasad N. G. and Shakarad M. 2001 *K*-selection, *α*-selection, effectiveness and tolerance in competition: density-dependent selection revisited. *J. Genet.* **80**, 63–75.

Kingsland S. 1995 *Modeling nature: episodes in the history of*

population ecology, 2nd edition. University of Chicago Press, Chicago.

Kishimoto K. 1990 Coexistence of any number of species in the Lotka-Volterra competitive system over two patches. *Theor. Pop. Biol.* **38**, 149–158.

Lawlor R. and Maynard Smith J. 1976 The coevolution and stability of competing species. *Am. Nat.* **110**, 79–99.

Léon J. A. 1974 *Selection in contexts of interspecific competition. Am. Nat.* **108**, 739–757.

Levin B. R. 1969 Genetic variability and competitive performance in *Drosophila. Genetics* **61**, s36–s37.

Levin B. R. 1971 The operation of selection in situations of interspecific competition. *Evolution* **25**, 249–264.

Levin S. E. and Udovic J. D. 1977 A mathematical model of coevolving populations. *Am. Nat.* **111**, 657–675.

MacArthur R. H. and Wilson E. O. 1967 T*he theory of island biogeography.* Princeton University Press, Princeton.

Mitchell P. and Arthur W. 1991 Extinction due to evolution of a competitor. *Evolution* **45**, 307–313.

Moore J. M. 1952 Competition between *Drosophila melanogaster* and *Drosophila simulans.* II. The improvement of competi-

tive ability through selection. *Proc. Natl. Acad. Sci. USA* **38**, 813–817.

Murray R. E., Parsons L. L. and Smith M. S. 1992 Competition between two isolates of denitrifying bacteria added to soil. *Appl. Env. Microbiol.* **58**, 3890–3895.

Parsons P. A. 1975 The comparative evolutionary biology of the sibling species *Drosophila melanogaster* and *D. simulans. Quart. Rev. Biol.* **50**, 151–169.

Pease C. M. 1984 On the evolutionary reversal of competitive dominance. *Evolution* **38**, 1099–1115.

Pease C. M. 1985 A coevolutionary isomorphism applied to laboratory studies of competition. *Evolution* **39**, 444–450.

Pimentel D., Feinberg E. H., Wood P. W. and Hayes J. T. 1965 Selection, spatial distribution and the coexistence of competing fly species. *Am. Nat.* **99**, 97–109.

Slatkin M. 1980 Ecological character displacement. *Ecology* **61**, 163–177.

StatSoft. 1995 *Statistica Vol. I: General Conventions and Statistics I.,* and *Vol. II: Statistics II.* StatSoft Inc., Tulsa, USA.

Thompson J. N. 1994 *The coevolutionary process.* University of Chicago Press, Chicago.