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Individual and group selection for productivity in *Tribolium castaneum*

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Summary. The usefulness of a non-random group selection method in the improvement of a character influenced by interactions among individuals has been experimentally tested in a population of *Tribolium castaneum*. The selected trait – number of adults produced in a fixed period of time – showed a clear increase after 11 generations of selection. This increase is related to a reduction in developmental time, and it was specific for the population structure in which selection was applied, vanishing when this structure was altered.

Key words: *Tribolium* – Intraspecific competition – Artificial group selection

Introduction

Competition has often been recognized as one of the most important components of productivity in many populations of cultivated plants (Mayo 1980), fish (Moav and Wohlfarth 1974; Busack 1983), and shellfish (Finley and Haley 1983). Therefore, the way in which selected individuals interact with their neighbors should be taken into account in the design of plants for the genetic improvement of productivity of such populations. Mather and Caligari (1981) developed a technique to analyze the kind and importance of these interactions, which has been applied by Hemmat and Eggleston (1988) in an artificial selection experiment with *Drosophila melanogaster*. However, this technique can only be used when identification of genotypes is possible, as occurs when two different strains or species are considered, and so cannot be used to study competition relationships between individuals of the same population.

Griffing (1967) proposed a theoretical model of artificial selection in populations of interacting genotypes. The model considered that each genotype in the population has effects of two different kinds: a direct effect on its own phenotypic value, and an associate effect on the phenotypic value of its neighbors. With individual selection, Griffing found that a positive selection intensity results in a negative response, when the covariance of direct and associate effects is negative and larger than the variance of direct effects. This result would be obtained if aggressive competitors were phenotypically superior to non-aggressive ones. Consequently, individual selection would increase competition intensity in the population and a decrease in productivity would ensue. On the other hand, group selection may lead to a positive response, because this procedure considers both direct and associate effects.

This situation has been detected in some experiments. Goodnight (1985) imposed artificial group and individual selection for increased and decreased leaf area in the cress *Arabidopsis thaliana*, and found that it responded to group selection and not to individual selection. He attributted this effect to interactions among individuals. Craig (1982) imposed group selection and individual selection for increased and decreased emigratory rate in *Tribolium confusum* and found that the interaction of population density with emigratory rate permitted a significant response to group selection, while individual selection was found to be ineffective.

Nevertheless, the variability of the random group means may be small and group selection may be inefficient. Griffing (1976 a, b, 1977) pointed out that the efficiency of the process can be improved with the use of non-random groups with increased genetic homogeneity. These non-random groups may, of course, be families and in such a case, group selection would be equivalent to family selection. However, the rationale of these two selection methods is different. Family means can be a useful selection criterion when individual environmental differences are randomly distributed (Falconer 1981). On the other hand, non-random group selection provides a way of identifying the most favorable associate effects in populations. These effects are similar for the members of the same family and, therefore, they will not cancel out when averaged over families.

The aim of this work is to test experimentally the usefulness of non-random group selection to improve one character affected by interactions among individuals. *Tribolium castaneum* was used because it has biological features that could result in a negative selection response to artificial individual selection for productivity. Population size is regulated to a large extent by interindividual interactions such as egg and pupa cannibalism (King and Dawson 1972), and there is genetic variability for the intensity of these interactions (Park et al. 1965; Mayes and Englert 1984). In addition, a negative covariance may exist between direct and associate effects of genotypes on productivity. Sonleitner (1961) has shown that females that are fed eggs as larvae may lay one more egg per day when adults than those that are not. Furthermore, Mertz and Robertson (1970) have observed that egg-eating accelerates larval development. Thus, cannibalism would have a positive direct effect on the productivity of individuals showing this behavior and a negative associate one on its neighbors. This negative relationship has also been found in interspecies competition experiments. Wade (1980) raised four *Tribolium castaneum* strains both in monoculture and mixed with *Tribolium confusum*. He observed that the better monoculture producers were the poorer interspecific competitors, with the situation reversed in the case of the low-producing strains.

Thus, a negative response could be obtained when positive individual selection for productivity was applied to a population of *Tribolium castaneum*. Actually, there is some experimental evidence in this direction. Wade (1976, 1977) studied the changes in productivity of *Tribolium* populations of different sizes, observing a continuous decline in population size over generations. McCauley (1978), Wade (1979), and McCauley and Wade (1980) analyzed the causes of this decline, and found that individual natural selection operates within those populations to increase the intensity of interference competition and, therefore, to reduce the number of adults produced.

Materials and methods

The beetles used to initiate this experiment were chosen at random from the Consejo laboratory strain of *Tribolium castaneum*, collected in 1964, near Madrid. The culture medium consisted of 95% whole wheat flour and 5% weight-dried brewer's yeast. Animals were maintained at 32 °C and 70% relative humidity. Two different populations were initiated and maintained with 50 pairs of adult individuals.

Vial populations

Each pair was placed in a vial with 1 g of culture medium and egg laying was allowed for 21 days; the pair was removed afterwards. The number of adult progeny in each vial was counted 14 days later and the ten most productive vials were selected. Five males and five females were randomly taken from each of these vials and mated at random, with the restriction that mating between individuals grown in the same vial was not allowed. Each of the 50 resulting pairs was placed in a vial containing 1 g of fresh culture medium, and another selection cycle was initiated. This is, therefore, the population in which non-random group selection is applied.

Bottle populations

There were three types maintained in exactly the same way, except that the amount of culture medium provided was different in each case (50, 25 or 10 g per bottle). One hundred adults were randomly taken from the base population and placed in a half-pint bottle with the corresponding amount of culture medium. As before, egg laying was allowed for 21 days. These progenitors were then removed and adult progeny was counted 14 days later. One hundred adults were randomly sampled from the progeny and introduced to a new bottle with the same quantity of fresh medium. This process was repeated each generation. The populations in these bottles were not subjected to artificial group selection, so that any change observed in their productivity should be ascribed to individual natural selection.

An additional type of population (test bottle) was maintained in order to obtain a direct comparison between the productivity of vial and bottle populations. In each generation, a random sample of 100 individuals from the vial population was introduced in a bottle with 50 g of fresh culture medium. This sample consisted of one adult male and one adult female from each of the 50 vials. This bottle had the same treatment as other bottles in the experiment, except that all the progeny obtained was discarded after being counted.

The experiment lasted for 11 generations and consisted of two replicates 1 week apart.

Results

The total number of adults produced per generation in each type of population is shown in Fig. 1 for the two replicates.

A linear regression of productivity on generation number was applied for each population. A positive significant slope was found in both replicates of the vial population (replicate I: $b = 82.04$, $t = 6.93$, $P < 0.01$; replicate II: $b = 57.79$, $t = 4.81$, $P < 0.05$) where non-random group selection was applied. The slope was non-significant in the bottle populations except for the 25-g bottle population of replicate II, where a small but significant positive trend was detected ($b = 8.16$, $t = 2.79$, $P < 0.05$). Obviously, smaller amounts of culture medium resulted in lower productivities, as shown by a comparison of 50-, 25- and 10-g bottle populations.

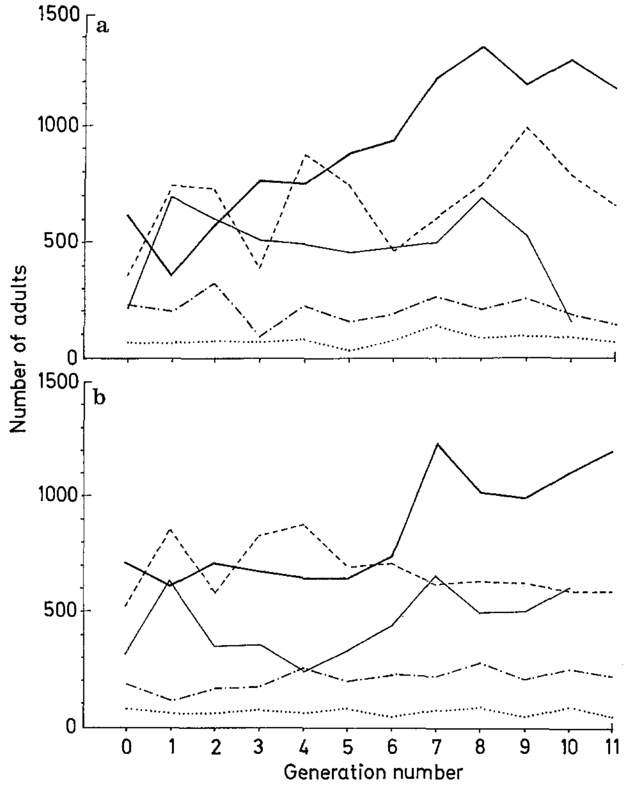

Fig. 1 a and b. Total number of adults produced at 35 days. Vials population (——), test bottle (——), 50-g bottle (- - - -), 25-g bottle (–·–·–) and 10-g bottle (······). **a** Replicate I; **b** replicate II

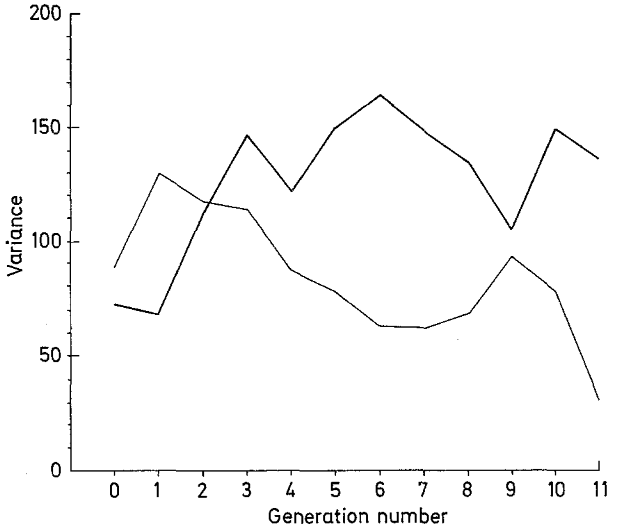

Fig. 2. Variance between vials for productivity in replicate I (——) and replicate II (——)

The most direct comparison between the group selection and non-group selection treatments is provided by test bottle and 50-g bottle. Their production of adult individuals over time was compared through the Wilcoxon signed ranks test (Siegel and Castellan 1988) and was found to be greater for the 50-g bottles in both replicates (replicate I: $T^+=42$, $P<0.10$; replicate II: $T^+=63$, $P<0.005$).

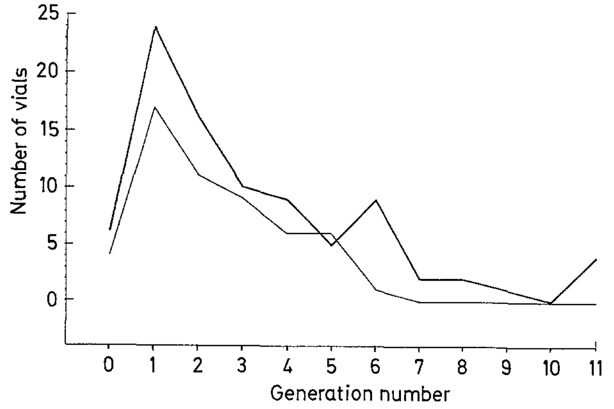

Fig. 3. Number of vials in which there were larvae and pupae but no adults after 35 days. Replicate I (——) and replicate II (——)

In the vial populations, realized heritabilities of productivity were calculated by regressing the population mean on the cumulative selection differential applied in each generation. They were $0.113+0.017$ in replicate I and $0.114+0.025$ in replicate II. The overall response was greater in replicate I, as larger selection intensities wer applied in this case. This difference in selection intensities could be explained by the evolution of the between-vial variance of productivity in both replicates, which increased with time in replicate I and decreased in replicate II (Fig. 2). When a linear regression was applied to these data, the slope was positive and approaching significance for replicate I ($b=5.00$, $t=2.21$, $P<0.05$) and negative and significant for replicate II ($b=-5.56$, $t=3.37$, $P<0.01$). A Student's t was used to compare the slopes of these two variances over time (Steel and Torrie 1980) and a significant difference was found ($t=19.97$, $P<0.001$). It is not easy to interpret this difference in variances, as individuals in both replicates were taken from the same population and treated in the same way.

This experiment was not designed to investigate which components of productivity could account for the observed response. However, it appears that the increase in productivity observed in the vial populations can be partially ascribed to a reduction in developmental time. The number of vials in which there were larvae and pupae but no adults after 35 days was recorded each generation (Fig. 3) and showed a continuous decrease throughout the experiment. Artificial selection may be the cause of this decline, as vials containing fast-developing individuals will tend to yield a greater number of adults in a fixed period of time than those with slow-developing ones. Thus, selection for increasing productivity will result in selection for fast development. It has been shown that developmental time of *Tribolium* can be modified by artificial selection (Dawson 1975; Soliman 1982). Similar results have been obtained in other insects as *Drosophila* (Marien 1958; Clarke et al. 1961).

Discussion

Vial productivity can be attributed to two types of components: those independent of interactions among individuals and those dependent on them. Among the first components are female fecundity and male reproductive ability. Their contribution to vial productivity depends on their expression in isolated individuals (i.e., the adult pair established in each vial) and they are, therefore, subject to individual selection. The second type of components – viability, developmental time, and cannibalism – affect productivity through their expression in non-isolated individuals, and they are consequently subject to group selection. For example, in our vial populations a cannibal female would eat its own eggs and would generally appear in low-production vials, which would be culled out by group selection.

As group selection was applied to all components of productivity that were affected by interactions between individuals, and as genetically homogeneous groups were used, the two requirements needed in Griffing's (1967) model to obtain an efficient selection method are met. The application of group selection assures a positive change in the population mean, and the use of non-random groups increases its efficiency. Thus, the clear response obtained in this experiment agrees with theoretical expectations.

However, selection did not result in an increase in productivity when the vial population structure was altered in the test bottle populations. Thus, it appears that productivity in single vials and productivity in large groups (i.e., test bottles) behave as two different characters. This may be due to different causes. Firstly, although the population density (measured as number of adults introduced per gram of culture medium) was the same in both populations, environmental conditions could have been different. Petrusewicz et al. (1963) have shown that the surface area and depth of available medium have a strong effect on *Tribolium* productivity, and these factors were not equal in vials and test bottles. The populations in vials lived in a large-surface shallow medium, whereas test bottle populations used a small-surface deep medium. Secondly, population density affects fecundity in *Tribolium* (Wade 1979) and its effect must have been different in each population, as the progenitor pairs were kept isolated in the vials but not in the test bottles.

Egg cannibalism is another possible explanation for the differences in productivity shown by vials and test bottle populations. It has been shown that the intensity of egg cannibalism by adults may depend on egg and adult genotypes (Mayes and Englert 1984; Englert and Raibley 1977). The mating pairs isolated in the vials had only their own eggs available to cannibalize, whereas the eggs laid by many unrelated individuals were available in the test bottles. As the genetic relationship among adults and eggs is different in vials and test bottles, cannibalism intensity can also be different in the corresponding populations.

The divergence observed between these two types of population does not contradict Griffing's (1967) model, but it emphasizes the importance of maintaining the population structure in order to profit from the genetic improvement obtained in the selected lines (Griffing 1968, 1977).

Productivity in test bottles was lower, too, than in 50-g bottle populations, which could be attributed to the origin of the adults used to initiate each type of bottle in each generation. Although adults in the test bottles were always raised in vials, those in the remaining bottle populations were raised in bottles every generation and, therefore, could have adapted to this circumstance. Furthermore, the conditions in which an individual grows affect both its fecundity and its cannibalistic behavior when adult (Boyer 1976). These conditions were different in test bottles and in bottle populations, and this could be responsible for some of the differences found in productivity.

The decrease in productivity observed by Wade and McCauley (1984) has not been found in our bottle populations. It is known that great interstrain variability exists in *Tribolium castaneum* for characters related to productivity. For example, Park et al. (1964) found clear differences in fecundity, duration of development, longevity, and cannibalism among four strains of this species.

The observed changes in the between-vial variance of productivity merit some discussion. The magnitude of this variance indicates that it must have been subjected to two opposing forces: artificial selection tending to decrease variability, and genetic drift tending to increase it. Wade and McCauley (1984) studied the genetic differentiation in productivity of populations of *Tribolium*, and found that the variance among populations increased with time, even in populations as large as 96, receiving 12.5% of migrants per generation. However, the conditions in our experiment were less favorable for population differentiation than those, as artificial selection was practised, and the migration rate (50%) was much higher. Consequently, it would be expected that the effect of artificial selection would have prevailed over that of drift and, therefore, the variance would have decreased. This was found in replicate I, which showed the clearer linear response to selection.

In conclusion, the selection method applied in this experiment has been effective, and it could be useful in the improvement of productivity in populations of cultivated plants and some domestic animals, provided that the population structure in which selection is carried out is maintained during the exploitation of the selected genotypes.

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