A CONFLICT BETWEEN DARWINIAN FITNESS AND POPULATION FITNESS IN *TRIBOLIUM* "COMPETITION" EXPERIMENTS

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THE coadapted gene pool of Mendelian populations arises as a result of natural selection and reflects the previous evolutionary history of the population. In such a population, the establishment of a superior mutant allele results not only in the replacement by the new allele of its predecessor but also in a reshuffling of many other genes and/or gene complexes. As the population undergoes this reshuffling period, many poorly adapted individuals may be produced. A similar trend would be expected to occur in the case of a new allele for which the heterozygote is superior to both homozygotes. In this case, the production of inferior homozygotes would continue even after equilibrium was reached.

In addition to the "substitutional load" (KIMURA 1960) imposed on a population from the replacement of inferior by superior alleles, an additional and even more important "load" may result from this reshuffling of the gene pool. The former cannot be thought of as placing a very substantial reproductive load on a population, whereas the latter could conceivably lead to a reduction in population fitness depending on the magnitude of coadaptation and gene interaction. During the course of a "competition" experiment between two species of *Tribolium*, a situation occurred which might serve as an extreme example of this process.

LERNER and DEMPSTER (1962) have postulated that one means of producing indeterminacy in the outcome of *Tribolium* "competition" experiments resides in unique events occurring in one of a series of replicate cultures. The situation to be described also provides an example of this type of event.

MATERIALS AND METHODS

The experiment from which the observations were derived has been described in detail elsewhere (DAWSON 1967). Briefly, a strain of *T. castaneum* (hereafter referred to as CS) that had been selected for fast development, measured as days from egg to pupa, for eleven generations, was placed in competition with a standard outbred strain of *T. confusum* (CF). Ten replicate cultures were established in eight dram shell vials containing stone-ground whole-wheat flour enriched with 5% brewer's yeast and kept in an incubator maintained at 29°C. and 40% relative humidity. These conditions are unfavorable for CS, which performs better in a warm, wet environment (PARK 1954; DAWSON 1967). Standard techniques were utilized in censusing and transferring the cultures at monthly intervals.

RESULTS AND DISCUSSION

In one of the ten replicate cultures, a recessive eye color mutant appeared in CS

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at the fourth transfer. The mutant, characterized by light brown eye color as opposed to the normal black, was subsequently shown to be allelic to chestnut (c), an autosomal recessive gene (EDDLEMAN and BELL 1963), and was given the symbol c^D .

Prior to the appearance of the c^D gene, CS seemed to be well on its way to eliminating CF (Figure 1). Ultimately, however, this trend was reversed, and the opposite result occurred.

The history of the c^D gene in the competition culture is given in Table 1 and Figure 1, from which it is seen that the frequency of c^D increased at the same time the percentage of CS in the vial was decreasing. Starting with the eighth transfer, at which time it appeared that the trend of competitive outcome was being reversed, all wild-type adults of CS were saved and individually mated to homozygous *chestnut* beetles to determine the numbers of $+/c^D$ and $+/+$ genotypes, which are also given in Table 1. These data reinforce the conclusion that the frequency of c^D was increasing as CS was being eliminated in competition. It is possible that an equilibrium was reached but the numbers are too small for more than speculation on this point.

If the increase in frequency of c^D resulted from selection for a new, more adaptive allele, and other results indicate that under these conditions c^D is superior to wild type, then the data may provide an extreme example of an unusual consequence of allelic substitution. It is suggested that individuals homozygous and/or heterozygous for c^D have a higher fitness than wild-type homozygotes in the

FIGURE 1.—Percentage of *T. castaneum* (CS; solid line) and the frequency of the c^D gene (dashed line) during the course of competition with *T. confusum*. The percentage of CS is plotted using a shifting two-point average in order to smooth out fluctuations in the curve which result from the technique of discarding adults at each monthly census (transfer).

TABLE 1

Numbers of CF and CS adults and of the three genotypes at the c^D locus at monthly transfers

Transfer	Number of		Number of			Frequency of c^D *
	CF	CS	+ / +	+ / c^D	c^D / c^D	
1	20	20	..	..	..	...
2	49	39	..	..	..	...
3	14	48	..	..	..	...
4	8	146	..	..	2	0.12
5	9	115	..	..	1	0.09
6	58	170	..	..	6	0.19
7	38	165	..	..	4	0.16
8	61	28	17	8	3	0.25
9	12	97	37	54	6	0.34
10	153	12	5	7	0	0.29
11	10	17	7	9	1	0.32
12	284	18	6	11	1	0.36
13	50	0	..	..	..	...

* Based on square root of frequency of mutant homozygotes for transfers 4 through 7.

unfavorable humidity used for this experiment. In the process of becoming established, the reproductive load imposed on CS as a result of numerous other changes in the gene pool was great enough to allow CF to overcome its apparent disadvantage and eliminate CS. CF was eliminated in the other nine replicate cultures, and in a control experiment involving the synthetic stocks of both species CF was eliminated in all ten replicates (DAWSON 1967).

WRIGHT (1959) and others have suggested that some genes may increase in frequency even when they decrease survival of the population. An example is the sterile t alleles in mice which are discussed by LEWONTIN (1962). However, in the latter case, a combination of distorted segregation ratios, random genetic drift, interdeme selection and migration are involved in maintaining the t alleles in natural populations. Another example has been described by CROSBY (1949) from studies on a homostyle allele in *Primula vulgaris*.

It should be pointed out that such drastic effects of allelic substitution as those envisioned above would undoubtedly not be observed in natural populations or even in most artificial laboratory populations, since most populations can easily tolerate a large amount of genetic death. However, in the intense interspecific competition between CS and CF in our cultures, a slight change in competitive ability of one species could lead to reversal of competitive outcome. Although the hypothesis I have outlined is somewhat radical, it is more reasonable than other alternatives, some of which will be considered below.

One explanation which has been suggested relates to the cannibalistic nature of *Tribolium*. Suppose that adults and/or larvae homozygous for c^D are more efficient at cannibalizing eggs than wild-type individuals, and further that there is a preference of the former for CS eggs. Then the frequency of the mutant gene would increase, but at the same time total fitness of CS would be reduced relative

to fitness prior to the occurrence of the mutant. This might be sufficient to provide CF with a great enough advantage to eliminate CS in competition. However, other data indicate that under the conditions of these experiments, there is no difference in intraspecific cannibalistic activity of mutant and wild-type individuals.

It has also been suggested that there may have been two or more simultaneous mutational events. For example, the relevant mutation may have occurred at another locus closely linked to c^D , so that the increase in frequency of c^D was only fortuitous. Alternatively, the relevant mutation, say $A_1 \rightarrow A_2$, may have occurred in CF. If A_2/A_2 and/or A_1/A_2 were sufficiently more cannibalistic on CS than A_1/A_1 to provide CF with superior competitive ability, but cannibalized $+/+$ preferentially to c^D/c^D and/or $+/c^D$, then the proportion of CS might decrease at the same time that c^D increased in frequency. Although this hypothesis also fits better with the established way of thinking about the course of natural selection, there is some indirect evidence that it is unlikely.

Previous attempts to select for competitive ability in CF have been unsuccessful (PARK and LLOYD 1955; LERNER and HO 1961). However, if this hypothesis were true, then it would follow that a new strain of CF established from the adults extracted from this culture should be superior in competitive ability to the original CF synthetic stock. The winning CF adults were saved and their progeny were utilized in competition against the CS synthetic stock at 29°C, 70% relative humidity. The new CF strain was eliminated in all 10 cultures and competitive ability, as measured by the mean number of transfers required for elimination, was 2.5 ± 0.2 compared with 5.3 ± 0.6 for the CF synthetic stock. Thus competitive ability was *lower* in the new CF strain, although the experiments were performed under different conditions.

One further, though less plausible, explanation may be sought in the size of the population present in this culture. Although the total number of CS adults recovered in the early transfers is fairly large (Table 1), the effective size (N_e) of the population is probably considerably smaller. Data from several species provided estimates of N_e ranging from 56 to 95% of the actual population size, with a mean of about 70% (CROW and MORTON 1955; KERR and WRIGHT 1954). In the present study this proportion is probably even smaller since the beetles counted and discarded at the time of transfer have eclosed throughout the previous month. Since the effective number is not known, and the population size in later transfers is small, the possibility of random genetic drift cannot be ruled out.

It is not, of course, known when the mutation to c^D first occurred. Mutant individuals have never been observed in the foundation population or in the selected line, either before or after the competition experiment was initiated. The possibility of contamination in this culture from the original c allele can be ruled out since no work with c was being carried out in our laboratory during the crucial time period.

Even if c^D was present in heterozygous form in one of the twenty parents used to initiate the culture, a high selective value of heterozygotes relative to wild-type homozygotes must be postulated in order to account for the frequency attained by the fourth month. Very rapid evolution under extreme conditions of environ-

mental stress has been observed in traits such as industrial melanism in moths (KETTLEWELL 1956) and DDT resistance in insects (CROW 1960), but it is hard to imagine that the conditions in the present experiments were that extreme.

A similar, though less spectacular result was observed in a related series of cultures which were also maintained in the unfavorable environment. The same two strains were utilized, although CS had been selected for fast development for 17 rather than 11 generations. Another eye color mutant was detected in CS at the 5th transfer in one of the ten cultures. Subsequent genetic tests established this mutant as an allele of red (r), a sex-linked recessive gene, and it was given the symbol r^D .

The pattern of elimination of CF in the culture and the frequency of the r^D gene, obtained directly from the proportions of normal and red-eyed males, are given in Figure 2. The initial stages of the elimination process are similar to those in the c^D culture (Figure 1). As r^D increased in frequency, the percentage of CS started decreasing, however, in this instance the species recovered and eventually eliminated CF. The average number of transfers required for elimination in 8 of the other 9 replicate cultures was 6.1, which is considerably less than the 14 observed in the culture where r^D was present. One remaining culture went for 46 months before CF was eliminated.

Although CF was eliminated in the r^D culture by the 14th transfer, the culture was maintained in the usual manner with only CS present. After 53 months, the

FIGURE 2.—Percentage of *T. castaneum* (CS; solid line) and the frequency of the r^D gene (dashed line) during the course of competition with *T. confusum*. The percentage of CS is plotted as in Figure 1. Frequency of r^D is based only on males.

r^D gene is still present at a fairly high frequency (Figure 2). It appears that a stable polymorphism has been attained in this small population.

Indeterminate outcome in *Tribolium* competition experiments has been reduced or eliminated in cultures where genetic variation in the competing species was adequately controlled (LERNER and HO 1961). However, unique stochastic events occurring in one of a series of replicate cultures may still lead to indeterminism (LERNER and DEMPSTER 1962). The two experiments described here provide a nice illustration of the occurrence of such unique events.

SUMMARY

During the course of a "competition" experiment involving the flour beetles, *Tribolium castaneum* and *T. confusum*, an eye color mutant appeared in *T. castaneum*. The frequency of the mutant gene increased and at the same time this species was eliminated from the culture, even though it was the winner in nine other replicates. It is suggested that the reproductive load placed on *T. castaneum* as a result of the reshuffling of the gene pool accompanying selection for the new allele may have been great enough to provide *T. confusum* with an advantage in competition. A similar, but less striking phenomenon involving a second eye color mutant was detected in another experiment.

LITERATURE CITED

- CROSBY, J. L., 1949 Selection of an unfavorable gene-complex. *Evolution* **3**: 212-230.
- CROW, J. F., 1960 Genetics of insecticide resistance: General considerations. *Misc. Publ. Entomol. Soc. Am.* **2**: 69-74.
- CROW, J. F., and N. E. MORTON, 1955 Measurement of gene frequency drift in small populations. *Evolution* **9**: 202-214.
- DAWSON, P. S., 1967 Developmental rate and competitive ability in *Tribolium*. III. Competition in unfavorable environments. *J. Stored Prod. Res.* **3**: 193-198.
- EDDLEMAN, H. L., and A. E. BELL, 1963 Four new eye color mutants in *Tribolium castaneum*. *Genetics* **48**: 888.
- KERR, W. E., and S. WRIGHT, 1954 Experimental studies of the distribution of gene frequencies in very small populations of *Drosophila melanogaster*. III. Aristapedia and spineless. *Evolution* **8**: 293-302.
- KETTLEWELL, H. B. D., 1956 Further selection experiments on industrial melanism in the Lepidoptera. *Heredity* **10**: 287-303.
- KIMURA, M., 1960 Optimum mutation rate and degree of dominance as determined by the principle of minimum genetic load. *J. Genet.* **57**: 21-43.
- LERNER, I. M., and E. R. DEMPSTER, 1962 Indeterminism in interspecific competition. *Proc. Natl. Acad. Sci. U.S.A.* **48**: 821-826.
- LERNER, I. M. and F. K. HO, 1961 Genotype and competitive ability of *Tribolium* species. *Am. Naturalist* **95**: 329-343.
- LEWONTIN, R. C., 1962 Interdeme selection controlling a polymorphism in the house mouse. *Am. Naturalist* **96**: 65-78.
- PARK, T., 1954 Experimental studies of interspecies competition. II. Temperature, humidity, and competition in two species of *Tribolium*. *Physiol. Zool.* **38**: 289-321.

- PARK, T., and M. LLOYD, 1955 Natural selection and the outcome of competition. *Am. Naturalist* **89**: 235-240.
- WRIGHT, S., 1959 Physiological genetics, ecology of populations, and natural selection. *Perspect. Biol. Med.* **3**: 107-151.