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The Genetic Basis of Egg Lay Response to Conditioned Medium in the Flour Beetle, *Tribolium castaneum.*

I. Two-Way Selection

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Summary. The rate of egg laying in *Tribolium castaneum* is affected by the quality of the environment and can thus serve not only as a component of fitness of the individual, but also as an adaptation to the long-term survival of the population. In an attempt to determine whether it is an independent genetic character, selection for high and low rates of response was carried out in beetles from three wild populations. When tests were done on virgin females, and responsiveness, corrected for scale effects, was used as the criterion for selection, separation between the lines was achieved in one generation. It is suggested that in natural populations of *Tribolium*, the responsiveness of the rate of egg laying to the quality of the environment is controlled by a small number of genes.

Key words: Rate of egg laying – Responsiveness to environment – Selection – Genotype x Environment interaction – *Tribolium*

Introduction

In flour beetles of the genus *Tribolium*, the rate of egg laying may be affected by two opposing selection pressures. In *T. castaneum*, according to Krause and Bell (1972), 75-80% of the phenotypic variation in fitness is determined by egg production, and natural selection is thus expected to favor higher rates, irrespective of the environment. At the same time, egg production may be involved in the adaptation of populations to long-term survival through its sensitivity to variations in the quality of the environment (Park 1935). In order to avoid overcrowding, and thus increase the probability of long-term survival, natural selection should favor increased responsiveness to the environment, with a reduction in egg production when environmental conditions deteriorate (Boyce 1946).

This apparent contradiction can best be solved, and a reasonable compromise achieved, if the rate of egg production on the one hand, and the responsiveness of egg production to the quality of the environment on the other hand, were controlled by two independent genetic systems. Unfortunately, while the genetic basis of egg production in *T. castaneum* has been dealt with in many studies (e.g. Orozco and Tagarro 1969; Carbonell and Fuentes 1973; Orozco and Bell 1974), the reduction in egg production in conditioned medium has been treated only from a physiological or an ecological point of view (Park 1936; Park and Woolcott 1937; Frey and Bell 1972). Nothing is known about its genetic basis and whether or not it is related to the level of egg production itself.

The present work presents the results of two-way selection experiments for responsiveness, carried out in three stocks, each derived from a different wild population of *T. castaneum* in Israel. These experiments suggest that responsiveness to the quality of the environment is indeed controlled by an independent genetic system, and that variability for this trait exists in all three populations examined.

Materials and Methods

(i) *Genetic Stocks.* Selection was carried out independently in the following three stocks which were derived from wild populations of *T. castaneum* from three different cities in Israel and named after them: Rehovot, Jaffa and Beer-Sheba. All the beetles that gave rise to a stock were collected together in a food plant or a grain store. The Rehovot stock was derived from 19 beetles that were collected one year before the beginning of the study, while the two other stocks were each established from over 100 individuals collected a few weeks before the study was started.

A fourth stock, derived from a synthetic population, was utilized in an independent, one-generation experiment. The synthetic population was established from beetles that were collected from all over Israel and had been maintained in the laboratory, in mass

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culture, for several years, with frequent additions of new beetles collected in the wild.

(ii) *Experimental conditions.* All experiments were carried out in the dark, in a Conviron (Controlled Environments Inc.) incubator, at a temperature of 29°C and 70% relative humidity.

The rate of egg laying was measured in three types of medium, representing three levels of quality of the environment, as follows:

1. Fresh medium. Whole wheat flour supplemented with 5g brewers yeast in 100g flour.
2. Mildly-conditioned medium ('mild medium'). As above, but after maintaining beetles at a density of about 50 per 100g medium for 3-4 weeks.
3. Highly-conditioned medium ('conditioned medium'). As in 1, but after maintaining beetles at a density of several hundreds per 100g medium for 2-3 months. In contrast to the first two types, the highly-conditioned medium is greyish and very fine-grained.

The three types of medium were prepared anew each generation, and the exact degree of conditioning, which was not controlled, varied from generation to generation.

(iii) *Experimental procedure.* In each generation the responsiveness of the various females in the selection lines and the control groups was estimated by testing each female successively in fresh medium, mild medium, again in fresh medium and finally in conditioned medium, according to the following schedule:

Age (days)	Step
0	the beetle, sexed as pupa, ecloses
1 – 7	maturing period
7 – 11	egg laying in 0.5g fresh medium (N_1)
11 – 14	accommodation period in mild medium
14 – 18	egg laying in 0.5g mild medium (N_2)
18 – 21	accommodation period in fresh medium
21 – 25	egg laying in 0.5g fresh medium (N_3)
25 – 28	accommodation period in conditioned medium
28 – 32	egg laying in 0.5g conditioned medium (N_4)
35	mating of beetles selected as parents for the next generation

In addition, the same schedule was employed in each stock, each generation, on a group of 20 beetles that were transferred always in fresh medium, and thus served for environmental control (EC group). Variation in the mean egg production of the EC group was considered to reflect changes due to age and to uncontrolled environmental factors.

Egg production was recorded as the mean number of eggs per day, counted after each 4-day period of egg laying, and corrected using the means of the corresponding EC group. The difference between the overall mean performance in the two tests in fresh medium served as additional correction for the past experience of the beetle, and was added to each value of N_2 and N_4.

(iv) *Definition and estimation of responsiveness.* In its simplest form, responsiveness can be defined as the difference between egg production in fresh medium and in conditioned medium, or as this difference relative to the performance in fresh medium. These definitions, however, are unsatisfactory because of the correlation which is commonly observed between inter-environment differences and mean performance. Using these definitions, selection for high responsiveness (a large difference between the performance in the two types of medium) may, in fact, be selection for high fecundity in fresh medium.

In order to demonstrate that responsiveness is an independent genetic character, it has to be shown that selection for or against responsiveness can be performed without affecting egg production in any consistent manner. For that purpose we chose as a measure of responsiveness, and thus as the criterion for selection, the value of β' as derived in the analysis of genotype X environment interaction by Moav and Wohlfarth (1974). The advantage of β' as a measure of responsiveness lies not only in the sytematic removal of scale effects from its calculation, but also in that it affords an estimate of the performance in a large variety of environments. Following is a brief review of the derivation of β':

In the conventional linear model, the performance of the j^{th} genotype in the i^{th} environment, g_{ij}, is partitioned into three components: The average environmental effect (a_i); the average genetic effect (g_j); and a genotype X environment interaction (ga_{ij}):

$$g_{ij} = a_i + g_j + ga_{ij}. \tag{1}$$

Bucio Alanis (1966) partitioned the genotype X environment interaction term into a linear function of the environmental deviation ($\beta_j a_i$) and a residual independent component (δ_{ij}), i.e.

$$ga_{ij} = \beta_j a_i + \delta_{ij}. \tag{2}$$

Combining equations (1) and (2) we get

$$g_{ij} = (1 + \beta_j)\,a_i + g_j + \delta_{ij}. \tag{3}$$

Thus β_j measures the response to systematic environmental changes. Moav and Wohlfarth (1974) have further partitioned β_j into two components which differ widely in their biological significance. The first is a consequence of the positive correlation, mentioned above, between inter-environment differences and g_j. This component cannot be considered a true genetic interaction. The second is the specific responsiveness of genotype j to environment i, independent of scale. The equation for this partitioning of β_j is

$$\beta_j = sg_j + \beta'_j. \tag{4}$$

s is the scale coefficient and β'_j is the net responsiveness of the j^{th} genotype to the underlying environmental variable. β'_j is thus the required measure of responsiveness, and for this reason we chose it as our criterion for selection. For each female, β' was calculated from the equation

$$g_{ij} = (1 + \beta'_j)\,a_i + g_j + sg_j a_i + \delta_{ij} \tag{5}$$

using as estimates for g_{1j}, g_{2j} and g_{3j} the corresponding net fecundity (NF) values, as follows:

$$NF_{1j} = \text{mean of } N_{1j} \text{ and } N_{3j}$$

$$NF_{2j} = N_{2j}$$

and

$$NF_{3j} = N_{4j}.$$

Because no objective criterion was available for estimating the average environmental effect, a_i was expressed, separately for each stock, as the average egg production of all the beetles in environment i. The subscript i takes three values – 1 for fresh medium, 2 for mild medium and 3 for conditioned medium.

The value of each β'_j was computed in two steps:

1. β_j was estimated for each beetle from the gross regression

of egg production (NF_{1j}, NF_{2j} and NF_{3j}) on the environment (expressed as a_1, a_2 and a_3. See equation (3)).

2. β'_j for the same beetle was calculated by correcting β_j for scale effects:

$$\beta'_j = \beta_j - sNF_{1j}.$$

The s value, one for each population, was estimated by regressing the various β_js on the corresponding values of NF_{1j}. For this reason it was the egg production in fresh medium (NF_{1j}) which was used in the derivation of β'_j from β_j. Note that β'_j could be derived with an s value for another environment, but in each case the NF value should correspond to the same environment as s. The s values in the present work varied between 0.01 and 0.1

(v) *Selection.* For each generation in each stock, the β'_j values were calculated for beetles belonging to one of the following three groups:

1. High response selection line (HR). Beetles selected for a relatively strong reduction of egg lay in conditioned medium (high β').
2. Low response selection line (LR). Beetles selected for a weak response to conditioned medium (low β').
3. Control group (C). Unselected beetles from the original stock.

In each stock, each selection line was continued every generation by five single-pair matings. Each mating contributed 4 daughters, and the values of β' were thus determined for each generation by the procedure described above, for a group of 20 females. In each of the HR lines the 5 females with the highest value of β' were selected as mothers for the next generation. The 5 females showing the lowest values of β' were similarly selected in each of the LR lines. While the females could be selected according to their individual performance, the males for the matings had to be selected on a family basis. The selected males in the HR lines were those whose sisters showed the highest mean values of β', while in the LR lines the males were selected from the families with the lowest mean values. The males were sexed as pupae together with their sisters, but were kept separately until the age of 35 days, when the matings were performed. In establishing the selected pairs care was taken to avoid full sib matings.

The controls were composed of groups of 20 females of the same age as the females in the selection lines. These beetles were derived from the unselected stocks which were kept in mass cultures. Occasionally it was impossible to collect the full number of pupae of the right age in these cultures and in these instances no controls were established.

In the first two generations of selection (S_1 and S_2), each of the tested females was kept in its vial together with a male, so that

Table 1. Net fecundity values (means and standard errors of the number of eggs layed per female per day) in fresh medium (NF_1), mild medium (NF_2) and conditioned medium (NF_3), in six generations of selection for high and low responsiveness in the Rehovot population. Values are given for all 20 females that were tested in each generation, and separately for the 5 females that were selected as mothers for the next generation. In S_1 and S_2, tests were performed on mated females. In S_3-S_5 the tested females were virgins. The females of S_6 were tested twice, first as virgins and then as mated females

		Low response selection line (LR)		High response selection line (HR)		
Generation	Parameter	Entire group of 20 females	Selected beetles	Entire group of 20 females	Selected beetles	Control
S_1 (mated)	NF_1	4.24 ± .44	4.47	4.81 ± .40	5.72	5.69 ± .48
	NF_2	1.94 ± .52	4.31	2.47 ± .47	−0.07	2.20 ± .49
	NF_3	0.99 ± .33	2.75	0.62 ± .22	−0.02	0.82 ± .25
S_2 (mated)	NF_1	4.75 ± .68	4.13	5.19 ± .38	5.32	5.90 ± .57
	NF_2	2.00 ± .25	2.15	1.97 ± .41	1.83	2.61 ± .31
	NF_3	2.22 ± .16	1.72	1.91 ± .13	−0.26	2.34 ± .22
S_3 (virgins)	NF_1	2.98 ± .21	3.25	2.82 ± .39	3.05	2.70 ± .28
	NF_2	2.53 ± .20	2.19	1.96 ± .19	2.34	2.24 ± .21
	NF_3	1.62 ± .15	2.63	1.10 ± .11	0.80	1.29 ± .18
S_4 (virgins)	NF_1	3.03 ± .31	3.20	1.75 ± .21	2.35	2.00 ± .40
	NF_2	0.73 ± .23	1.85	−0.10 ± .17	0.75	0.11 ± .25
	NF_3	0.78 ± .23	1.64	−0.11 ± .53	0.18	0.10 ± .12
S_5 (virgins)	NF_1	2.09 ± .29	2.55	1.92 ± .22	2.40	1.50 ± .26
	NF_2	1.16 ± .21	1.27	0.46 ± .11	0.27	0.74 ± .22
	NF_3	0.45 ± .18	1.43	−0.91 ± .11	−1.26	−0.01 ± .12
S_6 (virgins)	NF_1	5.04 ± .25		4.89 ± .28		3.26 ± .47
	NF_2	2.94 ± .26		2.84 ± .27		1.18 ± .27
	NF_3	2.40 ± .22		1.96 ± .26		0.12 ± .11
S_6 (mated)	NF_1	12.24 ± .64		10.53 ± .56		10.79 ± .65
	NF_2	8.69 ± .48		6.86 ± .78		6.44 ± .64
	NF_3	5.29 ± .31		4.12 ± .60		4.38 ± .61

selection was based on counts of eggs layed by mated females. Although the HR lines showed in these generations a higher response than the LR lines, the variance within each group was very large, and the differences between the two lines were not significant. As a result, starting from generation S_3, the counts were switched to eggs layed by virgin females. This change was in line with Yamada (1974), who showed that the genetic correlation between egg lay of virgins and that of fecundated females is 0.8, and Orozco and Bell (1974), who found that in selection for egg production, a large amount of the 'error variance' is removed if selection is based on virgins.

In generation S_6, at the end of the selection program, the beetles, after being tested as virgins, were mated and tested again. The effectiveness of selection performed on virgins was further tested by one generation of selection in the synthetic population.

Results and Discussion

The results of six generations of selection, performed in three independent stocks, are presented in Tables 1-4. Tables 1-3 include the means and standard errors of the numbers of eggs layed per female (mated females – generations S_1 and S_2; virgin females in generations S_3-S_6) in fresh medium (NF_1), mildly-conditioned medium (NF_2) and highly-conditioned medium (NF_3). These tables include also the means of the selected beetles of each generation. All calculations are based on the corrected values of egg production. Negative values of NF_2 and NF_3 were obtained in conditioned media when the actual rate of egg production was close to zero while in the corresponding EC (Environmental Control) group, egg production increased relative to the previous tests in fresh medium. Zero production when the environmental control group shows an increase should represent a stronger response than zero production without an increase in the controls. The correction values were usually in the range of 0-1 eggs, and the highest value reached was 1.75.

It is interesting to note that negative values of NF_2 and NF_3 occur only in the HR lines, meaning that these lines were closer to zero egg production in conditioned media. This fact was evident also when comparisons were made between the selection lines with respect to the numbers of beetles with zero egg production in conditioned media. In generation S_6, for example, no such females appeared in the LR lines, while the HR line of Beer-Sheba had 5, that of Rehovot had 3, and that of Jaffa – 1.

The responsiveness values (β') in the different lines and generations are listed in Table 4. Although the HR lines had higher values of β', compared to the corresponding

Table 2. Net fecundity values for the selection lines and control groups of the Jaffa population. For further details see legend of Table 1

		Low response selection line (LR)		High response selection line (HR)		
Generation	Parameter	Entire group of 20 females	Selected beetles	Entire group of 20 females	Selected beetles	Control
S_1 (mated)	NF_1	6.06 ± .46	6.55	6.35 ± .34	5.72	4.04 ± .42
	NF_2	2.86 ± .48	4.10	2.74 ± .46	−0.07	1.57 ± .32
	NF_3	1.97 ± .32	3.23	1.65 ± .32	−0.02	1.42 ± .19
S_2 (mated)	NF_1	5.29 ± .46	5.04	5.02 ± .57	5.32	4.93 ± .41
	NF_2	3.65 ± .38	3.66	2.97 ± .42	1.83	3.12 ± .40
	NF_3	1.88 ± .31	2.58	1.66 ± .33	−0.26	1.19 ± .21
S_3 (virgins)	NF_1	2.34 ± .23	1.95	2.55 ± .53	2.10	2.31 ± .64
	NF_2	1.94 ± .18	1.96	1.91 ± .24	−0.26	1.51 ± .40
	NF_3	1.01 ± .11	1.39	0.59 ± .14	−0.25	0.68 ± .27
S_4 (virgins)	NF_1	2.00 ± .14	2.60	1.56 ± .20	1.53	2.23 ± .25
	NF_2	0.76 ± .13	2.20	1.10 ± .35	0.44	0.83 ± .12
	NF_3	0.70 ± .19	1.09	0.39 ± .21	0.24	0.18 ± .76
S_5 (virgins)	NF_1	1.45 ± .19	1.85	1.50 ± .15	1.80	
	NF_2	0.97 ± .08	1.17	0.76 ± .12	0.37	
	NF_3	0.70 ± .19	2.09	−0.78 ± .13	−0.34	
S_6 (virgins)	NF_1	4.10 ± .34		3.19 ± .34		3.63 ± .63
	NF_2	1.70 ± .26		0.71 ± .21		0.85 ± .32
	NF_3	1.57 ± .25		0.31 ± .23		0.57 ± .32
S_6 (mated)	NF_1	9.48 ± .59		9.79 ± .54		8.89 ± 1.05
	NF_2	7.55 ± .54		7.35 ± .76		6.85 ± .64
	NF_3	4.81 ± .43		3.99 ± .45		4.66 ± .73

Table 3. Net fecundity values for the selection lines and control groups of the Beer-Sheba population. For further details see legend of Table 1

		Low response selection line (LR)		High response selection line (HR)		
Generation	Parameter	Entire group of 20 females	Selected beetles	Entire group of 20 females	Selected beetles	Control
S_1 (mated)	NF_1	5.16 ± .57	6.45	6.62 ± .73	8.55	6.38 ± .55
	NF_2	1.96 ± .28	3.01	1.76 ± .15	1.76	2.21 ± .34
	NF_3	1.06 ± .47	2.97	1.34 ± .32	1.62	1.62 ± .47
S_2 (mated)	NF_1	5.58 ± .42	5.75	5.33 ± .43	5.50	6.13 ± .63
	NF_2	3.42 ± .39	4.11	2.28 ± .34	1.58	3.06 ± .57
	NF_3	2.40 ± .39	3.23	1.98 ± .29	1.26	1.92 ± .34
S_3 (virgins)	NF_1	3.55 ± .30	3.45	2.55 ± .26	3.65	2.48 ± .44
	NF_2	2.54 ± .17	3.44	1.86 ± .14	1.95	2.07 ± .19
	NF_3	2.35 ± .25	2.59	1.29 ± .19	2.88	1.47 ± .23
S_4 (virgins)	NF_1	2.36 ± .30	1.80	1.69 ± .30	0.50	2.32 ± .58
	NF_2	1.56 ± .13	1.82	1.16 ± .11	0.88	1.77 ± .25
	NF_3	0.91 ± .15	0.05	0.45 ± .08	−0.25	0.68 ± .21
S_5 (virgins)	NF_1	1.80 ± .21	1.35	0.95 ± .10	1.25	
	NF_2	0.94 ± .15	1.09	0.32 ± .06	0.22	
	NF_3	0.27 ± .18	0.67	−0.04 ± .12	−0.77	
S_6 (virgins)	NF_1	4.82 ± .35		2.44 ± .31		
	NF_2	3.72 ± .24		1.28 ± .14		
	NF_3	1.54 ± .24		−0.39 ± .15		
S_6 (mated)	NF_1	6.59 ± .38		7.24 ± .52		
	NF_2	5.91 ± .45		4.88 ± .56		
	NF_3	4.08 ± .37		2.51 ± .42		

Table 4. Responsiveness values (means and standard errors of β′) of the various selection lines and control groups, in 6 generations of 2-way selection. LR: Low response selection line. HR: High response selection line. C: Control

	Generation						
Population and selection line	S_1 (mated)	S_2 (mated)	S_3 (virgins)	S_4 (virgins)	S_5 (virgins)	S_6 (virgins)	S_6 (mated)
Rehovot:							
LR-entire group	−.153 ± .09	−.278 ± .04	−.752 ± .10	.095 ± .09	−.061 ± .05	.931 ± .11	−.279 ± .04
selected females	−.632	−.397	−1.396	−.382	−.464		
HR-entire group	−.085 ± .07	−.185 ± .05	−.456 ± .07	.313 ± .05	.553 ± .05	1.012 ± .10	−.136 ± .04
selected females	.211	−.135	−.191	.582	.753		
C	−.080 ± .06	−.298 ± .06	−.564 ± .12	.244 ± .07	.150 ± .15	1.182 ± .08	−.173 ± .04
Jaffa:							
LR-entire group	−.049 ± .08	−.116 ± .09	−.117 ± .06	−.517 ± .10	−.384 ± .16	.056 ± .06	.009 ± .05
selected females	−.308	−.660	−.395	−1.170	−1.450		
HR-entire group	.153 ± .07	−.070 ± .07	.180 ± .06	−.397 ± .15	.238 ± .10	.346 ± .06	.156 ± .07
selected females	.211	.135	.362	.040	.559		
C	.048 ± .07	.053 ± .05	.040 ± .08	−.244 ± .05		.293 ± .07	−.029 ± .11
Beer-Sheba:							
LR-entire group	.131 ± .06	−.132 ± .09	−1.126 ± .19	−.565 ± .11	.336 ± .12	.272 ± .08	.615 ± .10
selected females	−.158	−.347	−2.510	−1.270	−.309		
HR-entire group	.230 ± .04	.027 ± .08	−.517 ± .14	−.251 ± .06	.657 ± .06	.481 ± .06	1.312 ± .08
selected females	.353	.260	.215	−.040	.912		
C	.132 ± .06	.073 ± .07	−.700 ± .16	−.378 ± .14			

LR lines, starting from the first generation of selection, a marked separation between the lines was achieved in generation S_3, after the counts were switched to those of eggs layed by virgin females. Selection continued for three additional generations, but the level of separation between the selected lines remained more or less unchanged. The fluctuations of the mean responsiveness from generation to generation can almost certainly be attributed to differences in the relative degree of conditioning of the mild and conditioned media in the different generations.

The results of the selection program support the suggestion that the responsiveness of the rate of egg production to the quality of the environment can be considered a genetic character. It now remains to be seen whether the choice of β' as the criterion for selection made responsiveness independent of egg production. A look at Tables 1-3 may suggest that this was not the case: Egg production in the LR lines is higher than in the HR lines not only in conditioned media, but also in fresh medium. However, this result is apparently not due to a correlation between responsiveness and egg production. First, the direction of the change in egg production is opposite to the one expected by the correlation. Second, comparisons for the rates of egg production between the females that were selected each generation as mothers for the next generation and the mean value of their line show that the selected beetles in only about one half of the cases in both the LR and HR lines had higher values than the unselected beetles. In the other half of the comparisons the order was reversed, suggesting that indeed no correlation exists between β' and egg production. Responsiveness, defined as β', can thus be considered an independent genetic character. The lower egg production of the HR females may be explained as being due to their super-sensitivity, even to the mild conditioning caused by their own presence. Sokoloff, Shrode and Bywaters (1965) noted that failure to supply beetles with fresh medium daily results in a drop in egg production.

The differences in β' between the selection lines were maintained, in all three populations, when the females that had been tested in generation S_6 as virgins were mated and retested as fecundated females (bottom parts of Tables 1-3). This suggests that the results of the previous generations are relevant also to natural conditions, and are not limited to egg production by virgin females. Note that in the fecundated state the phenomenon of higher egg production in the LR lines is nor reproduced.

In order to verify the possibility that one generation of two-way selection for β', using virgin females, is sufficient for achieving a separation between the selection lines, a single-generation experiment, using virgin females, was carried out in a fourth, synthetic population. The results of this experiment (Table 5) show that separation was indeed obtained after one generation, this time without two generations of selection of mated females preceeding the selection of virgin females, as was the case in the other three stocks.

Table 5. Net fecundity values and responsiveness (β') in the two lines of selection (LR and HR) and the control group (C), after one generation of selection on virgin females, in a synthetic population. For further details see legend of Table 1

Parameter	Low response selection Line (LR)	High response selection line (HR)	Control
NF_1	2.94 ± .31	3.65 ± .39	3.23 ± .36
NF_2	1.34 ± .25	0.63 ± .18	0.82 ± .23
NF_3	1.01 ± .18	0.41 ± .18	0.58 ± .26
β'	−.198 ± .07	.145 ± .05	.032 ± .07

In summary, our results indicate that, in *Tribolium casteneum*, the ability to respond to changes in the quality of the environment by changing the rate of egg production is an independent character, genetically distinct from the control of the mean rate in fresh medium. The fact that the separation between the lines was achieved in all populations after one generation of selection, and was maintained without further progress in subsequent generations, suggests that responsiveness, although a quantitative trait, may be controlled by a small number of genes.

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Literature

Boyce, J.M.: The influence of fecundity and egg mortality on the population growth of *Tribolium confusum* Duval. Ecology **27**, 290-302 (1946)

Bucio Alanis, L.: Environmental and genotype-environment components of variability. I. Inbred lines. Heredity **21**, 387-397 (1966)

Carbonell, F.; Fuentes, M.C.: Correlaciones genéticas de la puesta del *Tribolium castaneum* en diversos medios ambientes. Annales del Instituto Nacional de Investigaciones Agrarias, Madrid **2**, 73-82 (1973)

Frey, J.; Bell, A.E.: The effects of 're-used' media on fecundity and larval weight of *Tribolium. Tribolium* Information Bull. **15**, 75-76 (1972)

Krause, E.; Bell, A.E.: A genetic study of biomass in *Tribolium*. 1. Path coefficient analysis of base populations. Canad. J. Genet. Cytol. **14**, 181-193 (1972)

Moav, R.; Wohlfarth, G.: Magnification through competition of genetic differences in yield capacity in carp. Heredity **33**, 181-202 (1974)

Orozco, F.; Bell, A.E.: A genetic study of egg laying of *Tribolium* in optimal and stress environments. Canad. J. Genet. Cytol. **16**, 48-60 (1974)

Orozco, F.; Tagarro, P.: Respuesta a la selection y parámetros genéticos de la puesta de huevos en una estirpe de *Tribolium castaneum*. Boletin de Instituto Nacional de Investigaciones Agronomicas, Madrid **61**, 203-220 (1969)

Park, T.: Studies in population physiology. IV. Some physiological effects of conditioned flour upon *Tribolium confusum* Duv. and its populations. Physiol. Zool. **8**, 91-115 (1935)

Park, T.: Studies in population physiology. VI. The effect of differentially conditioned flour upon the fecundity and fertility of *Tribolium confusum* Duval. J. Exp. Zool. **73**, 393-404 (1936)

Park, T.; Woolcott, N.: Studies in population physiology. VII. The relation of environmental conditioning to the decline of *Tribolium confusum* populations. Physiol. Zool. **10**, 197-211 (1937)

Sokoloff, A.; Shrode, R.R.; Bywaters, J.H.: Productivity in *Tribolium castaneum*. Physiol. Zool. **38**, 165-173 (1965)

Yamada, Y.: *Tribolium* as a biological model in quantitative genetics. I Congress Mundial de Genetica Aplicada a la Produccion ganaderce **1**, 439-450 (1974)

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