A DYNAMIC STUDY OF GENOTYPE-ENVIRONMENT INTERACTION WITH EGG LAYING OF *TRIBOLIUM CASTANEUM**

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SUMMARY

Within-line family selection was carried out at an optimum (33°C) and two stress temperatures (28°C and 38°C) for increasing egg number laid by virgin females of *Tribolium castaneum* from the 7th to the 11th day after adult emergence. A control was maintained throughout the experiment. Two replicated lines were selected at each temperature and all selected lines were tested in each of the three environments.

Direct and correlated responses to selection in different environments have been analysed in order to study implications of genotype-environment interaction on the selection outcome. Although selection at the optimum environment has been the most effective it did not confer the specialisation needed for performance in stress environments. However, selecting in adverse environments led to a broader range of performance over environments, which in one case (38°C) included the optimum one.

The degree of adaptation to adverse environments was mainly determined by the magnitude of the genetic correlation between performances in the adverse and the optimum environments. The evolution of such correlations through selection has also been investigated.

1. INTRODUCTION

THE genotype-environment interaction ($G \times E$) problem has been recognised for many years (*e.g.* Haldane, 1946; Falconer, 1952). However, there is still discussion on what type of environment is optimal for a selection programme, and both theoretical and experimental studies have been carried out with the aim of developing a sound theory (Mather and Jones, 1958; Jones and Mather, 1958; Falconer, 1960; Dickerson, 1962).

There are two main experimental approaches to the problem: namely, static and dynamic. The static approach reveals the presence or absence of $G \times E$ interactions by the corresponding analysis of several genetic groups tested over a range of environments. The dynamic approach examines trends or changes of $G \times E$ interactions over several generations of directional selection. This could be of importance in a breeding programme in which predicted selection responses changed with corresponding changes in the $G \times E$ component.

In livestock, literature on the static approach is extensive (see Pani and Lasley, 1972, for a review). A few studies reported no $G \times E$ interaction, but in most cases a clear interaction was present. The latter suggest the possibility of special selection programmes aimed to produce specific strains suited to a given environment.

Several studies have been performed on the dynamics of $G \times E$ interactions

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through observations of the responses to selection under different environments in several experimental organisms: mice (Falconer and Latyszewski, 1952; Falconer, 1960; Bateman, 1971), *Drosophila* (Robertson, 1960), *Tribolium* (Bell and McNary, 1963; Hardin and Bell, 1967; Yamada and Bell, 1969), *Schizophyllum* (Jinks and Connolly, 1973, 1975; Connolly and Simchen, 1973).

This study presents results from 35 generations of selection using the flour beetle *Tribolium castaneum* as the experimental animal, egg number as the quantitative character, and temperature as the environmental variable. The evaluation of direct and correlated responses to selection in different environments, and the estimation of the $G \times E$ interaction and other genetic parameters, as well as their evolution through generations, was studied in order to add more information to the interpretation of the $G \times E$ phenomenon and its practical implications for animal breeders.

2. MATERIAL AND METHODS

The Consejo base population of *Tribolium castaneum* used in this experiment, as well as details on culture medium, management and material, have been described elsewhere (Orozco, 1969; Orozco and Bell, 1974a).

TABLE 1
Line designation

Levels of selection	Temperature of selection		
	28°C (F)	33°C (N)	38°C (T)
Selection for high egg number (A)	AF—I	AN—I	AT—I
	AF—II	AN—II	AT—II
No selection—Control (C)	CF—I	CN—I	CT—I
	CF—II	CN—II	CT—II

The quantitative character considered was egg production of virgin females, measured from the 7th to the 11th day after adult emergence. The changing environment was temperature, with an optimum (33°C) and two stress values, 28°C and 38°C, as cold and hot environments. The latter were applied only during performance testing and the preceding 48 hours. Otherwise, all individuals were kept at 33°C for the rest of their life-cycle.

From the Consejo base population three samples of size 1000 of each sex were taken and the females were performance tested in one of the three test environments (28°, 33° and 38°C). From each of these three samples one selected line (A) and a control (C) were started. All six lines were replicated twice. The line designations are shown in table 1.

In the A lines family selection was always practised and the populations consisted of 50 full-sib families. The egg-laying test was performed on 250 virgin females, five per family. After family means had been calculated, 10 families were selected, and 50 males and females (five of both sexes were selected per family) were mated to produce the next generation. Single pair matings were made at random, full-sib matings being avoided.

Control populations (C) consisted of 200 full-sib families. The egg-laying test was performed on 200 virgin females, taking one female at random from each family. These 200 females were mated in single pairs at random to 200 males which were taken from the 200 families (one per

family). When some families were lost, extra females and/or males were taken from other families in order to maintain 200 families, but with the restriction of never taking more than one extra individual per family.

An important part of this experiment was the performance test of every line in the two temperatures other than that in which it was selected. This test was made in odd generations, starting from the third, and 15 females per family were tested in the three temperatures (five in each temperature). The number of families tested was not always the total available since no more than 1000 to 1250 females could be evaluated in one test period. However, each family tested was always represented in all three environments.

3. RESULTS

(i) *The base population*

Some parameters of the Consejo base population at each of the three temperatures considered are listed in table 2. A more detailed description has been given by Orozco and Bell (1974a).

TABLE 2
The parameters of the base population

Parameters	Temperatures		
	28°C	33°C	38°C
Four-day laying average	12.94 ± 0.07	18.54 ± 0.11	14.84 ± 0.11
Phenotypic variance	77.60	158.54	158.19
Coefficient of variation (%)	68	68	85
Heritability:			
Sibs correlation (h_s^2)	0.33 ± 0.04	0.38 ± 0.04	0.35 ± 0.04
Offspring/dam regression (h_r^2)	0.26 ± 0.03	0.36 ± 0.03	0.30 ± 0.03
Dominance $\{2(h_g^2 - h_r^2)\}$	0.15 ± 0.06	0.04 ± 0.06	0.09 ± 0.06
Genetic correlation	28°-33°C 0.86 ± 0.02	28°-38°C 0.79 ± 0.03	33°-38°C 0.69 ± 0.04

The two stress temperatures (28°C and 38°C) caused a reduction in egg-laying as anticipated from preliminary studies (Fuentes and Orozco, 1970). The phenotypic variance at 33°C or 38°C is double the value found at 28°C. On the other hand, the coefficient of variation has the same value at 28°C and 33°C and it increases at 38°C. These facts illustrate the difficulty of choosing an appropriate scale for quantifying response patterns. The d^2 parameter estimates the contribution of the dominance variance plus a fraction of the epistatic variance.

Genetic correlations of the trait measured at the three temperatures considered show relatively high values, the largest being that for the correlation between 28°C and 33°C.

(ii) *Direct response means*

Mean egg-laying has been plotted against generation number in fig. 1 for each replicate of the *A* and *C* lines. As the control populations did not diverge between replicates nor show any time trends, and remained consistently stable over the course of the experiment, all calculations were carried out on uncorrected data.

FIG. 1.—Response to selection of *A* lines and performances of controls *C*. For line designations see table 1.

For convenience, the response to selection may be divided into three periods (generations 0-9, 10-20 and 21-35). In the *AN* and *AT* lines the initial response to selection has been maintained during the first period, the second being characterised by an attenuation of the response. In contrast, the *AF* lines showed a smaller but more uniform response throughout these two first parts of the experiment. The ranking order $AN > AT > AF$ was established from the start. It is interesting to note that while 38°C

FIG. 2.—Performance of each *A* line in the three environments (replicates pooled).
28°C ····; 33°C —; 38°C ----.

was a temperature stress for the base and control populations, the response in that environment was good and the *AT* lines seem to adapt themselves easily to the new temperature. On the other hand, the response to selection has been smallest in the *AF* replicates, and adaptation to the 28°C stress has not been as easy as adaptation to 38°C. In the third period (generations 21 to 35) a clear plateau was attained in all lines.

(iii) *Correlated response means*

In addition to the direct responses to selection, the results of testing each line in all three environments are presented in fig. 2.

The *AT* lines became well adapted to a selection environment (38°C) that imposed a distinct stress initially. Yet these *AT* lines also remained well adapted to 33°C, as demonstrated by their excellent correlated response in the latter temperature. Thus selection under stress has clearly broadened in this case the environmental range for optimum performance. These *AT* lines showed no such improved adaptation for the 28°C stress. In contrast, the *AF* lines adapted poorly to 28°C even though they were selected in this environment. For these *AF* lines, the optimum temperature remained 33°C, and the stress of 38°C appeared as no more detrimental than the temperature of selection. While the *AN* lines responded well to selection in the initially optimum temperature (33°C), the adaptation to stress (28°C or 38°C) was not improved over the course of the experiment, as shown by the parallelism of the responses, where it is clear that the rank order of the performances in the three temperatures is still the same as in the base population and 38°C still caused a real stress for these *AN* lines.

(iv) *Estimation of parameters*

Phenotypic variances and coefficients of variation were calculated and their changes during the selection process are presented in table 3. Full-sister and offspring-dam regression heritability estimates, plotted against

TABLE 3
Phenotypic variances and coefficients of variation (C.V.) for the selected lines at different generations. (Replicates pooled)

Generations	Variances			C.V. (%)		
	<i>AF</i>	<i>AN</i>	<i>AT</i>	<i>AF</i>	<i>AN</i>	<i>AT</i>
0	65.5	187.3	126.4	61	62	79
5	183.3	495.6	426.2	49	44	44
10	187.6	553.9	315.0	34	29	28
15	246.5	673.8	352.8	29	31	23
20	258.9	540.8	311.3	27	23	22
25	239.0	423.7	335.8	23	19	20
30	348.0	517.9	468.9	31	22	23
35	255.3	934.9	680.2	27	30	26

generation number, are presented in figs. 3 and 4, respectively, together with the linear regression slopes, for the first two periods in which the total number of generations of selection was divided. Estimates after generation 20, *i.e.* for the period of the plateau, are not included because, as must be

expected when additive variation is being exhausted, the distributions of individual values and of family means are then both far from normal, and intra-family variances are very heterogeneous, thus invalidating the analysis of variance technique. In lines *AN* and *AT* heritability has a clear tendency to decrease as selection progresses. In the *AF* lines it shows a slight reduction which is not statistically significant.

Genetic correlations between the performance of each line in each possible pair of environments have been calculated by sib-analysis. The

FIG. 3.—Full-sister heritability estimates of *A* lines for the first 20 generations (replicates pooled), with their linear regression on generation number. (** $P < 0.01$.)

FIG. 4.—Offspring-dam regression heritability estimates of *A* lines for the first 20 generations (replicates pooled), with their linear regression on generation number. (** $P < 0.01$.)

values per generation are very erratic, probably due to the large errors involved. The pooled estimates over the generation 11 to 19 of selection are presented in table 4 in order to study the trends after responses to selection became important. A decrease in magnitude of such correlations

TABLE 4
Genetic correlations between performances at two temperatures. (Pooled estimates over generations 11 to 19)

Lines	28°-33°C	28°-38°C	33°-38°C
<i>AF</i>	0.64 ± 0.08	0.48 ± 0.09	0.71 ± 0.06
<i>AN</i>	0.19 ± 0.18	0.13 ± 0.14	0.45 ± 0.14
<i>AT</i>	0.80 ± 0.05	0.38 ± 0.12	0.47 ± 0.11
Base population	0.86 ± 0.02	0.79 ± 0.03	0.69 ± 0.04

as selection progresses, except for two cases (*AF* 33°-38°; *AT* 28°-33°), can be observed by comparing the values for selected lines with the corresponding ones for the base population at the bottom of the table. Estimates after generation 20 were very imprecise even in the case of pooled estimates. This is not surprising considering that the genetic variances in the denominators of the correlation coefficients are sometimes close to zero.

(v) *Predicted and realised responses*

The percentage of families selected among the total number evaluated was not the intended 20 per cent, but 23, 26 and 27 per cent for the three periods considered. This produced the corresponding reduction of selection differentials commonly found in selection experiments when natural selection acts against the artificial selection imposed.

TABLE 5
Predicted and realised direct and correlated responses to selection. (Replications pooled)

Type of response	Lines and temperatures	Prediction		Realised responses	
		Predicted value	Efficiency	0 to 9	0 to 20
Direct	<i>AF</i> -28°C	4.27	0.58	2.46 ± 0.14	2.47 ± 0.05
	<i>AN</i> -33°C	9.36	0.69	6.46 ± 0.34	3.92 ± 0.18
	<i>AT</i> -38°C	7.24	0.86	6.21 ± 0.25	3.61 ± 0.18
Correlated	<i>AF</i> -33°C	5.18	0.75	3.88 ± 0.61	3.18 ± 0.20
	<i>AF</i> -38°C	4.35	0.86	3.76 ± 0.49	2.18 ± 0.28
	<i>AN</i> -28°C	3.91	1.01	3.96 ± 0.46	2.62 ± 0.21
	<i>AN</i> -38°C	4.89	0.95	4.64 ± 0.58	3.26 ± 0.27
	<i>AT</i> -28°C	3.03	1.03	3.12 ± 0.34	2.21 ± 0.15
	<i>AT</i> -33°C	4.51	1.14	5.12 ± 0.38	3.72 ± 0.25

Direct and correlated selection responses per generation, calculated by linear regression of average means on generations, are included in table 5 for generation-periods 0 to 9 and 0 to 20. Table 5 also contains the predicted selection responses for each line in the three temperatures. The corresponding efficiency of prediction, expressed as the proportion of the realised response measured over the predicted response, is also included. In calculating the efficiencies, only values for the first period studied have been

considered since, as has been shown in many selection experiments, predictions deteriorate after many generations of selection.

(vi) *Main and interaction effects*

From the response of each line in each environment after 20 generations, presented in table 5, main effects for lines and environments and interaction effects of the nine possible combinations of lines and environments were calculated, using the following statistical model:

$$Y_{ij} = \mu + L_i + E_j + LE_{ij},$$

where μ is the overall effect; L_i is the main effect for lines F , N or T ; E_j is the main effect for environments 28°C, 33°C or 38°C; and LE_{ij} the interaction effect for each of the nine combinations of lines and temperatures.

The process of a possible adaptation resulting from selecting in environments different to the one which is optimal for the base population can be examined by considering these main and interaction effects of lines and environments as shown in table 6. Each value of a realised response

TABLE 6
Main and interaction effects from direct and correlated responses at generation 20

Line	Temperature			Line main effects
	28°C	33°C	38°C	
<i>AF</i>	0.45	-0.02	-0.43	-0.41
<i>AN</i>	-0.07	0.07	0.00	0.25
<i>AT</i>	-0.38	-0.05	0.43	0.16
Temperature main effects	-0.59	0.59	0.00	

contains not only the gains of each line due to selection *per se* but also the positive or negative effect of the testing environment, plus the possible specific effect of testing the line in a particular environment (interaction effect). Of course, those nine figures are not independent and are only relative ones, so caution must be used in interpreting them. The rank order of temperatures in the base population is maintained for the whole selection experiment and the low performance of *AF* compared to *AN* and *AT* appears clear. Regarding the interaction effects, it should be noted that only the values in the diagonal are positive, indicating an adaptation of each line to its particular selection environment.

4. DISCUSSION

Direct responses to selection in the three environments have been, as expected, proportional to the magnitude of the heritabilities estimated in the base population. Correlated responses were smaller than the direct responses for *AN* and *AT*. The magnitude of the correlated responses was proportional to the product of the two heritabilities involved in the prediction, as the corresponding genetic correlations were large in all cases. The prediction of the responses to selection was in general good. This prediction was better for the correlated responses than for the direct ones,

a fact that may be due to the different degrees of precision of the estimates of genetic correlations and heritabilities. The intended selection intensity of 20 per cent was never achieved because natural selection was apparently acting against artificial selection through a reduction in fitness (Orozco, 1972).

(i) *Adaptation to adverse environments*

An examination of the interaction effects shown in table 6 makes it possible to deduce to some extent the accumulation of genetic effects favouring performance in specific environments. The large and positive interactions found for *AF*-28° and *AT*-38° and also the large but negative ones for *AF*-38° and *AT*-28° confirm that some accumulation of specific genetic effects favouring egg laying in each stress environment has taken place, with a corresponding deterioration of performance at the other extreme temperature. From the two negative interaction effects the conclusion could also be drawn that special genes for resistance to "stresses" common to both extreme temperatures either do not exist or have not been favoured by the type of selection practised. On the other hand, the small values obtained for *AN*-28°, *AN*-33° and *AN*-38° show no tendency to specialisation in these lines to their environment of selection, since the base population has already its optimum in that temperature. These data also indicate that selection in the original optimum does not change the relative performance in the three temperatures; this is also shown in the corresponding graph for the *AN* lines in fig. 2. The adaptation appearing from the interaction effects does not involve a perfect specialisation of lines *AF* and *AT* as measured from their total performances, since *AF* is not the best at 28°C, and *AT* at 33°C is equal to *AT* at 38°C.

The most interesting feature of the results obtained is the difference in the relative performance of each type of line in the three environments as shown in fig. 2. Selection in the optimum environment results in the best direct response and, after reaching the final plateau, egg laying in the three environments keeps the same ranking order as in the base population. However, the lines selected in stress present a very different pattern; while selection at 38°C produces a genotype performing nearly as well at this temperature as at the original optimum, with a low performance at 28°C, selection at the other stress temperature (28°C) produces genotypes with the best performance at 33°C and somewhat lower performances at the temperature of selection (28°C) and at the other stress temperature (38°C). This pattern of asymmetry compared with the symmetry obtained in the lines selected at the optimum demonstrates the presence of important $G \times E$ interaction effects.

The relative adaptation of *AT* for performance at 38°C and *AF* at 28°C can be interpreted in a simple way when observing the graphs of fig. 2. Since selection in the original optimum (33°C) has not resulted in a change in the relative performances at the three temperatures, the difference in the behaviour of the *AT* and *AF* lines is probably due to a tendency to adapt to each temperature of selection. This would be expected to result in a substantial upwards displacement of the corresponding plots for direct responses, as actually has happened; *AT*-38° has overtaken *AT*-33° and *AF*-28° has become equal to *AF*-38° but it has not yet surpassed the performance at 33°C.

(ii) *Genetic basis of adaptation*

If genes controlling egg laying in each of the three temperatures were totally different, *i.e.* the genetic correlations between the performances at each pair of temperatures were zero, a very easy adaptation and specialisation through selection in each of both stresses could have been possible and the performance of each line after several generations of selection would have been the best in its corresponding temperature of selection. On the other hand, if genes for performance in the three temperatures were the same, *i.e.* $r^G = 1$, lines selected in each of both stresses would have relative performances, when tested in the three temperatures, similar to the original ones in the base population. The best performance should then always be obtained at the original optimum. Obviously, intermediate situations such as those found here are the consequence of intermediate genetic correlations.

There appear to be no reports of perfect adaptation and specialisation being attained after selection in conditions different from the optimum for the base populations, so it is possible that cases with very low r^G do not exist. However, since studies where some adaptation was taking place were stopped before the "plateaux" were attained, it is not sure that this situation could not be found (Hardin and Bell, 1967; Yamada and Bell, 1969).

In the cases where no important genotype-environment interactions were detected, the genetic correlation should be nearly perfect, as happened in the experiments reported by Park *et al.* (1966) with rats and Dalton (1967) with mice, both for body weight and high- and low-quality diets. They both found that the gains made in each environment were independent of the environment of the selection. A similar conclusion was reached by Druger (1962) working with *Drosophila* wing length at different temperatures, where selection in one environment produced similar changes in the other environments. Unfortunately, no estimates of genetic correlations in the base population were given in any of those three studies.

In our base population many genes for performance must be common to all three temperatures as indicated by the high genetic correlations found. However, the genetic correlations were not perfect, showing that some specific adaptation occurred. The genetic correlation between performances in 33°C and 38°C was less than that obtained for 33°C and 28°C, and this could be the reason of the better adaptation obtained in *AT* as compared with *AF*.

In other experiments important $G \times E$ interactions were also found, suggesting that the result of a breeding programme is dependent on the environment of selection. Falconer (1960), working with mice, confirmed his previous results (Falconer and Latyszewski, 1952), concluding that growth on a high level of nutrition was equally increased when selection was made on a high or a low level; however, growth on the low level of nutrition was only increased when selection was made in this environment. Hardin and Bell (1967) and Yamada and Bell (1969) working with larva weight of *Tribolium* and varying diets, and Jinks and Connolly (1973) working with growth of *Schizophyllum* in varying temperatures, also found important $G \times E$ interaction trends which are very similar to those obtained in the present experiment. In both *Tribolium* experiments the magnitude

of the genetic correlation in the base population was intermediate and, therefore, some adaptation could be expected.

When analysing $G \times E$ interactions it is instructive to plot direct and correlated responses to selection against generation number by fitting linear regression equations. By doing so Yamada and Bell (1969) found a parallelism of the plots for the lines selected in the good environment and convergence of the plots selected in the poor environment; with these last two plots inside of the other two. In other words, it is possible to see that lines selected in the original optimum have a similar performance in both environments relative to those in the unselected population, whilst lines selected in the original adverse environment tend to converge in their relative performances in both environments. This situation also occurs in the data of Hardin and Bell (1967) and Jinks and Connolly (1973).

When comparing lines *AT* and *AN* of this experiment, an exactly similar trend is found, but in this case the performances of the lines (*AT*) selected at the "stress" temperature (38°) at 33°C and 38°C not only approach each other but even overlap (fig. 2). Since in the abovementioned cases it seems that the lines had not yet arrived at a selection plateau, it is reasonable to think that, at least in the *Tribolium* experiments, where $r^G = 0.60$, the converging plots might also have crossed if selection had been carried out for more generations (in our line *AT*, $r^G(33^\circ-38^\circ) = 0.69$). Comparison of *AF* with *AN* does not show a similar pattern, probably because the genetic correlation is higher ($r^G(33^\circ-28^\circ) = 0.86$).

The genetic architecture for general and specific sensitivity to environmental changes has been extensively studied in *Schizophyllum* by Connolly and Jinks (1975), who were able to establish the role of additive, dominance and epistatic gene action attributed to different components of growth and sensitivity. Since the present study is based on the responses to a within-line selection, only the additive fraction of specific genetic effects can be considered when discussing the possibilities of adaption to environments other than the optimum for the base population. Genes conferring general resistance to adverse conditions can also exist but probably are more of the overdominant type (Lerner, 1954) and so they could only be detected through a selection for combining ability scheme; as was the case with egg laying of *Tribolium* at different temperatures (Orozco and Bell, 1974*b*). The result from that reciprocal recurrent selection experiment together with those from the present work lead us to think that both specific and generic genes may be important for the expression of this egg-laying character in changing environments.

(iii) Genetic correlations trends

Genetic correlations between traits are expected to diminish under selection as a consequence of the fixation of the favourable alleles common to those traits. In this experiment the evolution of the genetic correlations between performance at different temperatures seems to be in agreement with the results obtained both for the direct as well as for the correlated responses to the selection.

Thus, it is verified (table 4) that only two correlations have not decreased: $r_{AF}^G(33^\circ-38^\circ)$ and $r_{AT}^G(28^\circ-33^\circ)$; cases where the temperature in which the line was selected is not included in the correlation. Also, the smaller

reduction of $r_{AF}^G(28^\circ-33^\circ)$ and $r_{AF}^G(28^\circ-38^\circ)$ compared with those in the corresponding correlations for AN and AT , respectively, is in agreement with the fact that AF gave lesser responses than AN and AT . On the other hand, the decrease of $r^G(33^\circ-38^\circ)$ was similar in both AN and AT .

The very drastic reduction of $r_{AN}^G(28^\circ-38^\circ)$ is difficult to interpret except by supposing that because of the good response to selection at 33°C , most of the favourable alleles for egg number at that temperature have been fixed and so the remaining non-fixed loci, which are those responsible for the genetic correlations observed, are those specific for lay at 28°C or 38°C , and then the genetic correlation is drastically reduced.

(iv) Conclusions

(1) When selection is carried out in an optimum environment the relative performances of the lines in other environments are maintained similar to those found for the unselected base population; therefore, special features for ideal performance in environments other than that optimum should not be expected. (2) Selection in adverse environments could produce responses in such a way that the genotypes of the selected lines had different performance from those found in the original population, when tested in the diverse environments of interest. (3) The genetic correlations between performances in optimum and in adverse environments, considered in the base population, are basic for understanding the $G \times E$ interaction problem; the smaller these correlations the larger would be the interaction effects. (4) These $G \times E$ interaction effects are expressed in a simple and logical way and probably they are even predictable as a function of the magnitude of the genetic correlation. (5) The possibility of a high adaptation or even a true specialisation of the line to the new environment depends not only on a very low genetic correlation (few genes in common) but also on a high heritability in that environment and, of course, on the number of generations of selection allowed to express that adaptation.

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