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Long -term selection for a quantitative trait in *Tribolium castenum*.2. Heritability and realized heritability

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ABSTRACT

An experiment with the flour beetle *Tribolium castaneum* was carried out to study the long-term response to selection for pupal weight for 20 generations. Three population sizes (10, 20 and 40 pairs of parents) and 3 proportions selected (10%, 20% and 30%) were considered along with a control for each population size. The experiment was replicated twice. Fullsib heritability estimates for pupa weight did not follow any definite trend with regard to population size or selection intensity. Pooled realized heritability estimates were 0.52 in period-1(1 to 10 generations) and 0.35 in overall period (1 to 20 generations). At the end of the experiment, the selected and one control line were assayed for the residual genetic variability. There was a reduction of 54 to 66 % in the heritability estimates measured from offspring-parent regression at the end of the experiment, compared to those estimated in the base population.

Key words: Heritability, Long -term selection,Quantitative trait, Realized heritability, *Tribolium castenum*

Selection experiments provide a dynamic approach to check the theoretical predictions of quantitative genetic theory and also evaluating realized heritability with direct reference to the base population. There has been some experimental evidence indicating that, in reality, the magnitude of heritability estimates is not constant over the phenotypic range of a population. Clayton *et al.* (1957) observed higher realized heritabilities at their most intense levels of selection than at lower selection intensities. The results of Frankham *et al.* (1968) indicated that the effect of selection intensity on realized heritability may be dependent on population size. Meyer and Enfield (1975) reported that the realized heritability estimates in the low direction became larger, while no trend was apparent over treatments in the high direction of selection. Further, they reported a marked asymmetry of heritability estimates. Gopikrishna and Taneja (1979), Gupta (1980) and Mudgal (1981) reported no apparent trend in the realized heritability as the selection intensity increased. The present investigation was undertaken to examine the long-term effects of selection using *Tribolium castaneum* as the animal model. Selection was carried out for heavier pupa weight measured on the day of pupation. The effect of selection, on the estimates of heritability (obtained from the fullsib correlation method) and realized heritability, was studied. After 20 generations of selection, the various lines were assayed for the remaining additive genetic variance. The estimates of heritability were compared to those in the base population.

MATERIALS AND METHODS

A synthetic population stock of *Tribolium castaneum* derived from 4 strains namely *Wild, Pearl, Black* and *Sooty*, obtained from Dr A E Bell, Purdue University, Lafayette, Indiana, USA, was utilized for this study. This population had been maintained in the Quantitative Genetics Laboratory in the Division of Dairy Cattle Genetics and Breeding at the National Dairy Research Institute, Karnal, Haryana, India, under random mating for about 20 generations. The nutrient medium consisted of 95% whole wheat flour enriched with 5% dried brewer's yeast.

Sex was differentiated at the pupal stage, using a binocular stereoscopic microscope. The age of the pupae was calculated by considering the day of mating as zero day. On the day of pupation, the pupae were sexed and weighed (in micrograms) individually, using a Mettler M-5 electric microbalance. The beetles were kept at a temperature of 33°±0.5°C with 70±3% relative humidity in a low temperature incubator (BOD incubator).

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The generation of base population has already been discussed in detail in the paper relating to response. The experimental design consisted of 3 population sizes (10, 20 and 40 pairs of parents) and 3 proportions selected (10, 20 and 30%) with a control for each population size. The experiment was replicated twice.

Analysis of the lines

At the end of the experiment, i.e. at generation-20, the lines were assessed for the presence of additive genetic variance. For this, 30 males and females in each line were picked up at random and mated in the ratio of 1:3. From each of these matings, 4 male and 4 female pupae were measured for pupal weight on the day of pupation.

Statistical analyses

The data generated were analyzed using Micro-2200 computer and Burroughs-4700 computer. The heritabilities for pupa weight in the base population and after 20 generations of selection were computed using the mixed-model least-squares and maximum likelihood computer program of Harvey (1976). Heritability was also estimated by various regression methods like regression of son on sire, regression of daughter on sire, regression of son on dam and regression of daughter on dam.

In each generation, heritability was also computed using fullsib correlation analysis.The generation means were regressed on the cumulative selection differential. The estimate of regression gave the realized heritability.

RESULTS AND DISCUSSION

The total duration of the experiment was bifurcated into 2 periods- Generation 1 to 10 (period-1), and generation 11 to 20 (period-2). In addition, an overall picture over the period of 20 generations was also examined.

Fullsib heritability estimates

The generation-wise heritability estimates did not exhibit any definite trend with regard to population size or selection intensity. The estimates fluctuated widely and had large standard errors. The coefficients of regression of fullsib heritability estimates on generation number, during periods 1, 2 and overall were mostly negative and nonsignificant. The statistically nonsignificant regression coefficients indicated that selection did not influence the fullsib heritability estimates over the 20 generations. Ruano *et al.* (1975) observed no overall change in fullsib heritability estimates during selection for rate of egg-lay in *Tribolium castaneum.* Daughter-dam estimates also gave similar results but their pattern of variation per generation was more erratic than that of full-sister estimates. The magnitude of heritability estimates was maintained throughout the experiment, although a nonsignificant reduction was observed in all but the 50% selection line at later stages of selection. Mudgal (1981) reported that the fullsib heritability estimates for pupa weight each generation, did not follow any consistent trend. The estimates fluctuated widely and had large standard errors. The author observed that there was a slight decline in heritability estimates in most of the lines, as evidenced by the regression of heritability estimates on generation number.

Realized heritabilities

The effects of selection intensity on realized heritability estimates were significant in both the periods (1 to 10 generations and 1 to 20 generations), while those of population size were nonsignificant. The realized heritability estimates exhibited a definite trend across the 3 selection intensities for a given population size (Tables 1, 2). The realized heritabilities increased as the selection intensity decreased. The estimates were highest under 30% and lowest at 10% selection intensity. Similar observations of increase in realized heritability estimates with the decrease in selection intensity have been reported by Rumball and Rae (1968), Meyer and Enfield (1975) and Mudgal (1981). In most of the selection experiments, the extent of agreement between the

Table 1. Realised heritability estimates for 1-10 generations

P	Rep	Selection intensities			
		10%	20%	30%	Pooled
10	R-1	0.4295±0.0268	0.4959±0.0441	0.6201±0.0733	0.4628±0.0219
	R-2	0.5100±0.0275	0.5568±0.0284	0.5903±0.0577	0.5387±0.0187
	RP	0.4687±0.0192	0.5389±0.0239	0.6017±0.0453	0.5066±0.0142
20	R-1	0.4002±0.0235	0.5059±0.0394	0.5608±0.0540	0.4442±0.0189
	R-2	0.4564±0.0238	0.5583±0.0211	0.5990±0.0258	0.5368±0.0135
	RP	0.4279±0.0167	0.5466±0.0186	0.5919±0.0233	0.5055±0.0110
40	R-1	0.4606±0.0231	0.5267±0.0292	0.6461±0.0317	0.5254±0.0157
	R-2	0.4921±0.0263	0.5091±0.0299	0.6309±0.0458	0.5201±0.0181
	R1	P.4743±0.0174	0.5181±0.0209	0.6412±0.0261	0.5232±0.0119
Pd.	R-1	0.4305±0.0140	0.5142±0.0207	0.6237±0.0256	0.4854±0.0106
	R-2	0.4834±0.0149	0.5459±0.0147	0.6045±0.0209	0.5328±0.0094
	RP	0.4554±0.0102	0.5352±0.0120	0.6122±0.0162	0.5119±0.0070

P, Population size; Rep, replicates;RP, replicates pooled; Pd, pooled.

Table 2. Realised heritability estimates for 1-20 generations

P	Rep	Selection intensities			
		10%	20%	30%	Pooled
10	R-1	0.3164±0.0129	0.3227±0.0195	0.3781±0.0294	0.3254±0.0101
	R-2	0.3366±0.0198	0.3545±0.0245	0.3525±0.0282	0.3457±0.0135
	RP	0.3224±0.0108	0.3350±0.0153	0.3648±0.0204	0.3326±0.0081
20	R-1	0.3120±0.0109	0.3372±0.0188	0.3669±0.0197	0.3274±0.0085
	R-2	0.3155±0.0147	0.4112±0.0178	0.4483±0.0190	0.3790±0.0097
	RP	0.3132±0.0088	0.3762±0.0129	0.4091±0.0137	0.3499±0.0064
40	R-1	0.3230±0.0128	0.3897±0.0130	0.4679±0.0207	0.3741±0.0083
	R-2	0.3605±0.0149	0.3225±0.0166	0.4331±0.0200	0.3645±0.0097
	RP	0.3389±0.0097	0.3642±0.0102	0.4499±0.0144	0.3700±0.0063
Pd	R-1	0.3166±0.0070	0.3612±0.0094	0.4079±0.0128	0.3447±0.0057
	R-2	0.3375±0.0093	0.3619±0.0109	0.4240±0.0124	0.3664±0.0061
	RP	0.3242±0.0056	0.3616±0.0071	0.4163±0.0089	0.3536±0.0039

P, Population size; Rep, replicate; RP, replicates pooled; Pd, pooled.

expected and realized heritability estimates is often poor. Since one of the important uses of heritability estimates lies in their ability to predict response to selection, it is useful to have reliable estimates prior to the onset of the selection experiment. Realized heritability estimates accurately measure the response to selection but are available only after the fact. On the other hand, expected estimates, usually based on the resemblance between relatives can be obtained in advance, but are of practical value only if they accurately reflect the realized heritability. Rumball and Rae (1968) observed that the realized heritability declined more rapidly where selection was strongest. Meyer and Enfield (1975) observed that realized heritability estimates in the low direction became progressively smaller as the proportion selected increased. However, no trend was apparent in the high direction of selection.The authors concluded that the progress relative to selection intensity was greater for downward than for upward selection and that more intense the selection in the downward direction the larger was the realized heritability. The realized heritability estimates exhibited a consistent trend in lines where the total number of individuals scored was the same. In this case also, the estimates of realized heritability increased as selection intensity decreased, viz. 40 (20%) >20 (10%) and 20 (20%) > 10 (10%). Such an observation was also made by Frankham *et al.* (1968) while experimenting with *Drosophila*. Dempster (1955) was of the opinion that selection intensities nearer to 50% would allow response to continue for longer, and thus perhaps give a greater total response than higher selection intensities. The overall estimates of realized heritability (pooled over the replicates) in the present study was 0.512±0.007 for 1 to 10 generations. This estimate declined to 0.354±0.004 for the period 1 to 20 generations. The overall estimate of 0.354 for 1 to 20 generations is in agreement with the estimates between 0.33 and 0.35 reported by Wilson *et al.* (1963), Enfield *et al.* (1966) and Gall (1971). Gall (1971) reported a mean realized heritability of 0.34 in lines selected for heavier pupa weight for the period 1 to 10 generations. This estimate declined to 0.28 for the period 1 to 15 generations and 0.25 for the period 1-23 generations. At the end of the experiment, the average realized heritability was 0.23 (0 to 30 generations). The estimate of realized heritability during the first period in this study (0.512) is closer to the estimate of 0.54 of the base population (son-sire and daughter-sire regression). This strong agreement would allow reasonable faith to be placed in heritability predictions at least in short-term selection. Such an agreement was also obtained by Enfield *et al.* (1966). These authors reported that the realized heritability estimates and the heritability obtained from the components of variance analysis and sire-offspring regression were the same. Large population size, in their study, led to more refined estimates of heritability and simultaneously reduced the effects of inbreeding on realized progress. On theoretical grounds, the expected and realized heritability measure the same thing and should thus be in close agreement.An implicit assumption is that heritability of the trait within a population is constant at any point in time and is uniform over the phenotypic range of population. Accordingly, the expected heritability based on resemblance between relatives should be the same regardless of the portion

Table 3. Comparison of heritability estimates at the beginning and end of the experiment

Method	Base	End of the experiment population	
		Control	Selected lines
	h^2±SE	h^2±SE	h^2±SE
Sire-son	0.54±0.05	0.44±0.08	0.21±0.04
Sire-daughter	0.54±0.05	0.45±0.08	0.25±0.04
Dam-son	0.57±0.05	0.38±0.11	0.20±0.03
Dam-daughter	0.58±0.05	0.41±0.11	0.20±0.03
Fullsib component	0.75±0.06	0.75±0.10	0.44±0.02
Sire component	0.63±0.11	0.52±0.18	0.16±0.04
Dam component	0.86±0.08	0.85±0.16	0.64±0.05

of the distribution that is observed. Falconer (1955) pointed out that the realized heritability is expected to be the same, regardless of the direction of selection, particularly in early generations of selection, in populations initially at intermediate gene frequency. The author also mentioned that the estimates of realized heritability were very little biased by the effects of scale and natural selection. Rahnefeld *et al.* (1963) discussed reasons for considering the heritability of a trait separately for the 2 sexes. If there is a lack of perfect genetic correlation between a particular trait measured in the 2 sexes, then the realized heritability estimates would be expected to be smaller than the estimates from statistical analyses, assuming that other sources of bias have been removed. The genetic correlation between the 2 sexes in the base population in this study was very high (0.996), thus obviating the need for estimating heritability sex- wise.

Analyses of lines

At the end of generation-20, the different lines were assayed for the presence of the remaining additive genetic variance. The lines were assayed both by a hierarchical design and offspring-parent regression. Heritability was estimated from components of variance and regression analyses. The estimates of heritability from the components of variance at the end of the experiment when compared with those in the base population revealed that there was a decline in the estimates on account of selection (Table 3).A reduction to the extent of 54 to 66 % was observed in the estimates from offspring-parent regression.Comparison of the pooled estimates of heritability from components of variance analysis and offspring-parent regressions with those of the control at the end of the experiment, revealed that the estimates in the selected lines were much lower than those in control lines. The control, being a population with no selection, takes care of any time-trends and can be compared with the selected lines to obtain a true profile of the genetic variability. The lower estimates of heritability at the end of the experiment in the selected lines when compared to those in the base population and controls, indicated that selection had utilized the additive genetic variance over the 20 generations and the fixation of genes for heavier pupa weight has taken place, thus leading to a decline in the heritability. Ruano *et al.* (1975) estimated heritabilities by an appropriate design at the end of the experiment and reported a marked decrease in the magnitude of the heritability estimates. The authors associated the progressive reduction in additive genetic variance with the observed attenuation of selection response.

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