Original article

Genetic interaction between sire and population of mates in *Drosophila melanogaster*

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Summary – A model experiment was set up to examine the level of genotype–environment interaction existing between a sire and the population from which its mates were drawn. The character considered was left sternopleural bristle number in *Drosophila melanogaster*. A total of 128 males, scored for the trait, were mated to females of the same and another strain. The characteristic was then measured in both the pure and crossbred progeny and the heritabilities for the trait in each group were determined. The genetic correlation between pure and crossbred performance ($\pm$ standard error) estimated from covariances, 0.59 ($\pm$ 0.17), was found to be significantly different from one, indicating the presence of genetic interaction. The heritability of purebred performance (by regression analysis) was found to be 0.29 and the heritability of crossbred performance 0.11. The corresponding average values from sib analysis were 0.40 and 0.24, respectively. A comparison of responses from different selection methods, incorporating the estimated parameters, found that selection on the basis of sire's own performance led to the largest improvement in the performance of crossbred progeny. The implications of the results are discussed.

genotype–environment interaction / genetic correlation between purebred and crossbred performance / sternopleural bristles / *Drosophila melanogaster*

Résumé – Interaction génétique entre géniteur et population des partenaires chez *Drosophila melanogaster*. *Une expérience modèle a été menée pour examiner l'importance de l'interaction entre le géniteur et la population dont ses partenaires sont issus. Le caractère utilisé est le nombre de soies sternopleurales sur le côté gauche chez* Drosophila melanogaster. *Cent vingt-huit mâles, contrôlés pour le caractère, ont été accouplés à des femelles de la souche elle-même et d'une autre souche. Les héritabilités ont été estimées dans les 2 souches. La corrélation génétique entre les caractères en souche pure et en croisement, de 0,59 ± 0,17, était significativement différente de 1, indiquant la présence d'une interaction génétique. Les héritabilités du nombre de soies chez les souches*

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pures et hybrides sont 0,29 et 0,11 respectivement par régression parent-descendant et les valeurs correspondantes estimées par analyse des germains sont 0,40 et 0,24. Une comparaison des réponses prédites selon différentes méthodes de sélection, sur la base des paramètres estimés, montre que la sélection sur la performance propre du géniteur donne l'amélioration la plus grande de la performance dans la descendance croisée.

interaction génotype–milieu / corrélation génétique entre performance pure et croisée / soie sternopleurale / *Drosophila melanogaster*

INTRODUCTION

The value of crossbreeding to increase the efficiency of production has been recognised in many animal species. The improvement of production in the crossbred is due primarily to the manifestation of heterosis, or hybrid vigour, which indicates the presence of non-additive gene effects.

Standal (1968) suggests that if heterosis is due to overdominance then selection on the basis of purebred performance will not result in corresponding improvement in the crossbred. Selection on the basis of crossbred performance, or combining ability, is complex. In practice such a scheme will be difficult to use, particularly when populations are small. If the degree of genetic interaction occurring between a sire and the population of females to which it is mated is quantified, then the choice of the optimal selection method is facilitated.

It is possible to determine the extent of genetic interaction present using 2 methods. The interaction may be statistically estimated from parameters obtained within a single generation (Brun, 1982), as in this case, or derived from estimates of variances and covariances realised in the course of selection (Brun, 1984).

Brun (1982) defined parameters to statistically estimate the degree of genetic interaction for the particular situation of genotype by mate interaction within a single generation. These parameters are the genetic correlation between pure and crossbred performances (rg_{pc}) and the relative heritability of purebred performance (h_p^2) compared with the heritability of crossbred performance (h_c^2). The parameters reflect the different means by which the interaction may be expressed: in one case, as a change in the ranking of sires, or in another, as a difference in variance between the purebred and crossbred progeny.

Should a large genetic interaction be discovered, then selection on the basis of crossbred performance will result in greater genetic progress. Should the interaction be absent, or insignificant, then selection within the purebred may be regarded as the method of choice.

When the genetic interaction is not significant, most of the gene effects expressed in the purebred will also be expressed in the crossbred progeny. Selection that considers only performance in the purebred is desirable since it relies only on individual performance rather than on a progeny test which may reduce selection intensity and increase generation interval.

In this study, progeny variances were analysed to estimate genetic parameters including the genetic correlations between pure and crossbred performance, correlations between progeny and sire performance, and the relative heritabilities for

pure and crossbred performance for left sternopleural bristle number in *Drosophila melanogaster*. The parameters were obtained with the aim of elucidating the optimal method of selection for the improvement of crossbred progeny performance.

MATERIALS AND METHODS

Two random breeding strains of *Drosophila melanogaster* were employed as source and tester stocks. The source stock contributed the experimental sires and the dams for purebred progeny, and the tester stock provided dams for crossbred progeny. The source stock used was the Hunter Valley wild-type strain and the tester stock a white-eyed mutant strain. Both stocks were maintained as separate random mating populations.

At intervals of less than 12 h newly emerged flies were separated into sexes for each strain type. Once separated, these flies were transferred to fresh bottles containing a semolina-based fly medium. Males of the source strain were chosen at random, scored for left-sternopleural bristle number, and placed in separate numbered vials with 4 females each of their own and the tester strain. After 4 d the males were discarded and the females placed in pairs of similar strain into laying vials labelled with the sire number and a label distinguishing that pair. Prior to the emergence of progeny, females were removed from the vials and discarded.

A total of 150 sires were measured in 3 groups, 1 group in each of 3 successive months. It was planned to score left sternopleural bristle number in 10 progeny, 5 of each sex, for each progeny vial. In all 128 sires were included in the analysis.

The sire components of variance for the 4 progeny classes, 2 for each strain and 2 for each sex, were calculated using a hierarchical analysis of variance for unbalanced data. The model was adjusted for the effects of group (fixed), sire (random), vial (random) and random error according to the model:

$$Y_{ijkl} = \mu + g_i + s_{ij} + v_{ijk} + e_{ijkl}$$

where:
Y_{ijkl} = individual bristle score;
μ = progeny mean for each sex and strain type;
g_i = effect of the ith group;
s_{ij} = effect of the jth sire within the ith group;
v_{ijk} = effect of the kth vial within the jth sire and the ith group;
e_{ijkl} = random error term.

By analysing the data separately for sexes, the presence or absence of sex dimorphism (Frankham, 1968) could be established.

Progeny class regressions were analysed. Coefficients were obtained for crossbred on purebred performance, within and between sexes, and also for progeny bristle score on sire bristle score according to the model:

$$Y_{ij} = \mu + g_i + b(x_{ij} - \bar{x}) + e_{ij}$$

where:
Y_{ij} = progeny mean over vials for the jth sire of the ith group of the dependent variable (which may be any progeny class);

μ = progeny mean for each strain and sex type;

g_i = effect of group;

b = regression gradient;

x_{ij} = independent variable, which may be sire bristle number, purebred male bristle number, or purebred female bristle number;

$\bar{x}$ = mean bristle number for the progeny classes compared;

e_{ij} = random error term.

The regressions were used to determine covariances between offspring and parent for each progeny class and for purebred and crossbred performance. Variances and standard errors for the covariance estimates were calculated.

Estimation of the interaction between sire and population of mates

Heritabilities

Narrow-sense heritabilities were determined by regression analysis with the heritability for any progeny class being regarded as twice the progeny on sire regression. Half-sib analysis was used to estimate the heritability for left sternopleural bristle score from partitioned components of variance, such that:

$$h^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_v^2 + \sigma_e^2}$$

for any progeny class. Standard errors were calculated according to the method of Falconer (1983).

Genetic correlation between pure and crossbred performance

The pooled genetic correlation was estimated from variances and covariances pooled over crossbreds (V_c) and purebreds (V_p), and between pure and crossbreds (cov_{pc}) according to the equation:

$$rg_{pc} = \frac{cov_{pc}}{\sqrt{V_p \times V_c}}$$

where:

rg_{pc} is the pooled genetic correlation between pure and crossbred performance;

$V_p = [\sigma_{Spm}^2 + \sigma_{Spf}^2]/2$;

$V_c = [\sigma_{Scm}^2 + \sigma_{Scf}^2]/2$;

$cov_{pc} = [cov_{Spmcm} + cov_{Spfcf} + cov_{Spfcm} + cov_{Scfpm}]/4$;

σ_{Spf}^2, σ_{Spm}^2, σ_{Scf}^2, σ_{Scm}^2 are estimated sire components of variance for purebred females, purebred males, crossbred females and crossbred males, respectively; and cov_{Spmcm}, cov_{Spfcf}, cov_{Spfcm}, cov_{Scfpm} are covariances between sire components for the same progeny classes.

The variance for the correlation was calculated as the variance of a ratio (Kempthorne, 1957):

$$\text{var}(rg_{pc}) = \frac{V_A}{BC} + \frac{rg_{pc}^2}{4}\left[\frac{V_B}{B^2} + \frac{V_c}{C^2}\right]$$

where

$A \quad = cov_{pc}$;
$B \quad = V_p$;
$C \quad = V_c$;
$V_A \quad = 0.0625[\text{var}(cov_{Spfcf}) + \text{var}(cov_{Spfcm}) + \text{var}(cov_{Spmcf}) + \text{var}(cov_{Spmcm})]$;
$V_B \quad = 0.25[\text{var}(\sigma^2_{Spf}) + \text{var}(\sigma^2_{Spm})]$;
$V_C \quad = 0.25[\text{var}(\sigma^2_{Scf}) + \text{var}(\sigma^2_{Scm})]$.

The pooled correlation enabled the expected level of interaction between the 2 breed types to be assessed without special regard to sex.

Direct and correlated selection responses for increased crossbred performance

The ratios of the correlated response per generation to individual selection, and the correlated response to selection on purebred progeny performance against direct selection on the performance of crossbred progeny were calculated.

$$\frac{CR_i}{R_c} = \frac{i_1}{i_2} \times \frac{h_p}{h_c} \times rg_{pc} \times \sqrt{\frac{4 + (n-1)h_c^2}{n}}$$

$$\frac{CR_p}{R_c} = rg_{pc} \times \frac{h_p}{h_c} \times \frac{\sqrt{4 + (n-1)h_c^2}}{\sqrt{4 + (n-1)h_p^2}}$$

$CR_i \ = $ correlated response in crossbred progeny from selection on sire;
$CR_p \ = $ correlated response in crossbred progeny from selection of sires on purebred progeny test;
$\ R_c \ = $ direct response from selection of sires on crossbred progeny test;
$\ \ n \ = $ number of progeny tested per sire;
$\ \ i_1 \ = $ standardised selection differential for individual selection;
$\ \ i_2 \ = $ standardised selection differential for progeny tested sires.

Comparisons were made on the basis of selecting 50 sires from groups of 1 000, 2 000, 4 000, 10 000 and 20 000 individuals tested. If sires were progeny tested then fewer sires could be tested. Selection intensity was reduced as the number of progeny tested per sire increased.

RESULTS

Partitioning of variance components

Sire components for purebred progeny were approximately double those for crossbred progeny. Group and sire effects were significant in all progeny classes. The vial effects were insignificant for all progeny classes (table I).

Table I. Components of variance estimated from hierarchical analysis of variance.

| | | Variance component | | |
Progeny class	σ^2 within	σ^2 vial	σ^2 sire	σ^2 group
Purebred female	1.300	0.000	0.177	0.102
Purebred male	1.366	0.053	0.118	0.234
Crossbred female	0.940	0.022	0.063	0.020
Crossbred male	0.994	0.031	0.060	0.150

Heritability of left sternopleural bristle score

The heritability for left sternopleural bristle number in the crossbred was lower than that for the same character in the purebred (table II). This difference is due to lower sire components of variance for crossbred progeny of both sexes. The heritabilities calculated for crossbred progeny are not strictly narrow sense heritabilities since differences exist in levels of dominance and gene frequencies between the purebred and crossbred populations.

Table II. Heritabilities of purebred and crossbred performances.

Method of estimation	Sib analysis $h^2 \pm SE$	Regression analysis $h^2 \pm SE$	Pooled regression h^2
Purebred female	0.48 ± 0.117	0.37 ± 0.102	
Purebred male	0.31 ± 0.095	0.21 ± 0.105	0.29
Crossbred female	0.25 ± 0.097	0.10 ± 0.085	
Crossbred male	0.22 ± 0.094	0.12 ± 0.101	0.11

Genetic correlations between pure and crossbred performance

The pooled estimate for the genetic correlation between pure and crossbred ($\pm$ standard error) was 0.59 (± 0.17) (table III). The estimate differed significantly from one at the 5% level. The estimates were similar for all sex–breed combinations.

Table III. Genetic correlations between pure and crossbred performance*.

Genetic correlation	$rg_{pc} \pm SE$
Crossbred female with purebred female	0.41 ± 0.30
Crossbred male with purebred female	0.66 ± 0.39
Crossbred female with purebred male	0.62 ± 0.41
Crossbred male with purebred male	0.72 ± 0.46
Pooled genetic correlation between pure and crossbred	0.59 ± 0.17

* rg_{pc} denotes the genetic correlation between purebred and crossbred progeny performances, and SE denotes the standard error.

Estimated response ratios

Estimations revealed that in most cases individual selection of the sire's own performance gave a superior response in the progeny to direct selection on crossbred progeny performance, which was in turn superior to selection on the basis of purebred progeny performance (table IV). Differences in heritabilities for pure and crossbred progeny contributed to this result, as did the reduction in possible selection intensity with progeny testing, offsetting the benefits of increased selection accuracy.

Table IV. Ratio of response to selection on individual sire performance (CR_i) and selection on purebred progeny performance (CR_p) against direct selection on crossbred progeny performance (R_c), assuming that 50 sires are selected and a limited testing capacity.

Ratio	Testing capacity	Number of progeny per progeny-tested sire		
		5	10	20
$CR_i R_c$	1 000	1.46	1.75	∞
	2 000	1.28	1.24	1.55
	4 000	1.19	1.06	1.08
	10 000	1.12	0.95	0.87
	20 000	1.08	0.90	0.80
$CR_p R_c^*$	> 1 000	0.89	0.83	0.77

* Ratio independent of testing capacity.

DISCUSSION

Genetic interaction between sire and partner population has been found to occur with greater frequency in traits related to fitness and heterotic traits, which usually have low heritability, than in traits with additive gene action (Brun, 1985).

This study found the genetic correlation between pure and crossbred ($\pm$ standard error) to be significant (0.59 ± 0.17), supporting the hypothesis of non-additivity. Left sternopleural bristle number usually behaves in an additive manner and exhibits little or no heterosis. It was, therefore, surprising to find that the heritability for the trait in the purebred was higher than that in the crossbred. Such a difference is often an indicator of non-additive gene action.

Estimates of heritability for bristle number in *Drosophila melanogaster* are wide, ranging from 0.14 (Sheridan *et al*, 1968) to 0.46 (Howe and James, 1973). The estimate of heritability from regression analysis in the purebred (0.29) agrees well with the expected heritability of 0.2–0.3, while that from sib analysis was somewhat higher than expected (0.40). The regression analysis estimate for the crossbred (0.11), is clearly lower than was to be expected from previous studies while the sib-analysis estimate (0.24) was in the expected range.

No estimate for genetic interaction between sire and mates has been previously reported for sternopleural bristle number in *Drosophila* using the statistical approach. Results in other animals and traits have indicated various levels for rg_{pc},

ranging from less than zero to greater than 1. The few values for laboratory insects are scattered widely (-0.32, 0.85 in Brown and Bell (1980) for eggs laid in *Drosophila melanogaster*, and 0.4 for pupal weight in *Tribolium casteneum* (Wong and Boylan, 1970)).

The comparison of responses from individual selection in sires, and selection on the basis of purebred progeny, and crossbred progeny performances when testing resources are limited, revealed that under the observed conditions ($rg_{pc} = 0.59$, $h_p^2 = 0.29$, $h_c^2 = 0.11$) there was little benefit in the use of progeny testing as an aid to selection for increased crossbred performance. With limited testing capacity, selection on individual sire performance was found to generate superior response to that from selection on the basis of crossbred progeny performance, which was in turn superior to selection on the performance of purebred progeny. This was primarily due to the higher selection intensity possible using mass selection, and to a reduced dependence on sire prolificacy.

The accuracy of progeny testing is increased with the number of progeny tested per sire. However, when testing capacity is limited, increasing the number of progeny tested per sire decreases the number of sires able to be represented in the test. If the number of sires required is fixed, then the selection intensity is decreased as the number of progeny per sire increases. The optimum response from direct selection on crossbred progeny performance occurs at the point of balance between effects on selection accuracy and selection intensity. As testing capacity is increased, the response from direct selection on crossbred performance increases relative to the response from individual selection due to increased selection accuracy.

Robertson (1957) showed that the optimum response from progeny testing was achieved when the number of progeny (n) tested was:

$$n = \frac{0.56\sqrt{k}}{h_c^2}$$

where k describes the ratio of males recorded to the number selected and h_c^2 is the heritability of crossbred performance.

The comparison of purebred and crossbred progeny testing to improve crossbred performance revealed that for every testing capacity and family size, direct selection on crossbred performance yielded superior responses in the crossbred to those resulting from selection on the basis of purebred progeny performance, a direct result of the genetic interaction between pure and crossbred performance.

The use of progeny testing to evaluate sires for crossbreeding performance in livestock is disadvantaged by some practical considerations. First, it is necessary for the breeder to maintain both source and tester dam populations in order to progeny test the sires. One of the dam populations will produce stud stock (source), and the other commercial stock (tester). Different management practices may be required for the 2 types of stock. Second, there is a loss of production in purebred progeny when sires are selected for crossbreeding merit and a significant genetic interaction is present. Finally, the selection lag occurring as a result of progeny testing reduces selection response, particularly in larger species. The genetic gains able to be made through direct selection on crossbred progeny performance are unlikely to outweigh these disadvantages.

Harris (1976) suggests that the optimal selection approach is to select on an index of sire and crossbred progeny performance. An alternative approach may be to select sires for progeny testing on the basis of their own performance and then make a further selection on the performance of their progeny, or on an index of individual and progeny performance (Cochran, 1951). In this case crossbred progeny would be used in the progeny test.

Although a genetic interaction between the sire and population of mates was observed, it was insufficiently large to warrant direct selection for crossbred progeny performance. This was demonstrated by the comparison of responses between individual selection and selection on the performance of crossbred progeny. The findings suggest that for both genetic and economic reasons, selection on the basis of individual performance is the best selection method of those examined, assuming that the correlation between pure and crossbred performance is a positive one.

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