Theor Appl Genet (1986) 72:388-394

Effects of assortative mating for pupa weight on genetic parameters of unselected *Tribolium castaneum*

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Received December 3, 1985; Accepted February 26, 1986
Communicated by D. Van Vleck

Summary. Effects of random (R) or positive assortative (A) mating for pupal weight (PW) on genetic parameters of pupation time (PT), pupal and larval weights (LW) were studied in unselected populations of *Tribolium castaneum.* Two groups, each with 50 males mated to 100 females in each of 5 replicates, were either R-mated or A-mated for 3 generations. Genetic parameters were estimated from covariances between sibs (R group) or by an iterative method (A group). Estimates of heritability in R and A groups were 0.30 ± 0.12 and 0.39 ± 0.02 (PW); 0.26 ± 0.13 and 0.49 ± 0.04 (LW); and 0.39 ± 0.10 and 0.25 ± 0.03 (PT). Estimates of genetic correlations in the R group were – 0.21 ± 0.23 (PW and LW); 0.45 ± 0.10 (PW and PT); and – 0.77 ± 0.14 (LW and PT). Those in the A group were 0.27 ± 0.10 (PW and LW); 0.15 ± 0.14 (PW and PT); the genetic correlation between LW and PT was not estimable in this group. Within-family variances (grams squared) of PW by generation (1, 2, and 3) were, respectively: 0.048 (R) and 0.047 (A); 0.054 (R) and 0.041 (A); and 0.050 (R) and 0.046 (A). In agreement with theory, estimates of heritability of PW and LW were larger in the A group. Estimates of genetic correlations in the A group were inconsistent with expectations from theory. Assortative mating tended to decrease within-family variance of PW.

Key words: Assortative mating – Genetic parameters – *Tribolium castaneum*

Introduction

Effects of systems of mating on means, variances and covariances are of importance in animal breeding theory and applications because these parameters play a major role in selection. Positive assortative mating, the mating of individuals who are more similar phenotypically than if they were chosen at random from the population, is one such mating system.

Rao and Narain (1967), in a one-locus model with complete dominance, found that the mean of a population decreased following one generation of assortative mating; the decrease was proportional to a decline in heterozygosity. With two loci and complete dominance, the mean decreased more after assortative mating when there was linkage than with free recombination. With no dominance, assortative mating had no effect on mean value. Crow and Felsenstein (1968) showed that assortative mating for a trait affected by a large number of loci would have little effect on the mean of a population, irrespective of dominance.

Crow and Felsenstein (1968); Vetta (1976) and Bulmer (1980) argued that dominance (D) and environmental (E) components of variance do not change appreciably, if at all, with assortative mating. In the absence of epistasis, the variance of a quantitative trait (P_{t+1}) under assortative mating can be written (Crow and Felsenstein 1968) as

$$P_{t+1} = A_{t+1} + D + E \tag{1}$$

where A_{t+1} is the additive genetic variance after $\underline{t}$ generations of assortative mating. Further (Crow and Felsenstein 1968)

$$A_{t+1} = [(1 + \varrho h_t^2) A_t + A_0]/2 \tag{2}$$

where ϱ is the phenotypic correlation between mates, h_t^2 is heritability at generation $\underline{t}$, and A_0 is the additive genetic variance under random mating. The change in variance from assortative mating thus stems from an increase in additive genetic variance which, in turn, depends on ϱ and on h_t^2. At equilibrium (Felsenstein 1981)

$$P = \frac{A}{1-r} + D + E \tag{3}$$

where P and A are equilibrium variances, and r is the equilibrium genetic correlation between mates (ϱh^2). It follows that with assortative mating, the phenotypic variance and heritability increase monotonically until reaching equilibria. This is important because response to selection is proportional to $\sqrt{P}$ and h^2.

Effects of assortative mating for trait X on covariance between X and Y were deduced by Reeve (1953, 1961); Latter (1965) and Gianola (1982). The correlation between relatives for Y increases following assortative mating. The correlation between X (Y) in a relative and Y (X) in another relative also changes with assortative mating (Gianola 1982), the direction of the change depending on the sign of the equilibrium genetic correlation between X and Y. Assortative mating could be used to manipulate genetic variance-covariance matrices, correlated responses to selection and the efficiency of selection (Gianola 1982; Fernando and Gianola 1984).

The objective of this study was to investigate the effects of positive assortative mating for pupa weight in unselected *Tribolium castaneum* on genetic parameters of larval and pupal weights and pupation time.

Experimental procedures

An outbred population of *Tribolium castaneum*, Purdue "f" Foundation, was used in the study. A sample of approximately 1,600 individuals was obtained from the Population Genetics Institute. Purdue University, and introduced to the University of Illinois, where it was maintained in an incubator at about 32 °C and 70% relative humidity. A medium containing 95% all purpose wheat flour and 5% dried brewers yeast was used.

Upon introduction, the unsexed stock was divided at random into 5 sets, each with approximately 320 individuals. Following a 7-day mating period, eggs were collected at day 8 and a random sample of 120 larvae was taken from each set at day 13. Individual larvae were weighed and placed in vials, and pupation weight and time were recorded as each individual pupated. Then, 20 adult males and 40 adult females were randomly chosen within each set of 120 individuals, yielding a total of 100 males and 200 females. The above procedure was replicated five times by conducting additional egg collections in the foundation stock.

In each of the five replicates, males and females were randomly divided into random (R) and assortative mating (A) groups, each with 50 males and 100 females. Individuals in R were mated at random (2 females per male) and those in A were mated assortatively (2 females per male) based on pupa weight. The "best" male was mated to the "best" two females, and so on. R and A groups were closed and propagated for three generations, always mating 50 males to 100 females in each group and following the appropriate mating system without intentional selection of parents. Full-sib and half-sib matings were avoided.

Larval and pupal weights in micrograms, and pupation time were recorded. Larval weight (LW), was taken 13 days after egg collection. Pupal weight (PW), was taken within 24 hours of pupation; pupation time (PT) was the number of days between egg collection and pupation.

Methods of analysis

Random mating group

Correlations between sibs were obtained following a decomposition of variance and covariance (Method 3 of Henderson 1953) using the model

$$y_{ijkl} = \mu + t_i + s_{ij} + d_{ijk} + w_{ijkl} \tag{4}$$

where

y_{ijkl}: record on progeny l from dam k mated to sire j in generation-replicate i;
μ: fixed effect common to all individuals;
t_i: fixed effect of generation-replicate subclass i ($i = 1, \ldots, 15$);
s_{ij}: random effect of sire j in generation-replicate i;
d_{ijk}: random effect of dam k dam mated to sire j in the generation-replicate i, and
w_{ijkl}: a random residual peculiar to individual i j k.

The following assumptions were made: $E(y_{ijkl}) = \mu + t_i$, $E(s_{ij}) = E(d_{ijk}) = E(w_{ijkl}) = 0$, $\mathrm{Var}(s_{ij}) = \sigma_s^2$, $\mathrm{Var}(d_{ijk}) = \sigma_d^2$ and $\mathrm{Var}(w_{ijkl}) = \sigma_w^2$. Further, to simplify computations, sire, dam and residual effects were assumed to be mutually uncorrelated so that

$$\mathrm{Var}(y_{ijkl}) = \sigma_s^2 + \sigma_d^2 + \sigma_w^2 . \tag{5}$$

Because sires and dams in generation $\underline{t}$ were progeny of sires and dams used in generation $\underline{t-1}$, the assumption that sire and dam effects are uncorrelated within and across generations is expected to lead to bias in the estimates of variance components. Taking account of the potential bias requires the specification of large additive relationship matrices of sires and dams. Because the bias is probably very small (e.g., Van Vleck and Hudson 1982), it was felt in this case that the additional computational effort required to remove it was not warranted. Variance and covariance components were then estimated by equating the mean squares and products arising in the usual analysis of variance of (4) to their expectations, ignoring relationships. Heritability and genetic correlations were estimated using sire, dam or sire plus dam components of variance and covariance. Standard errors of the estimates of heritability and of genetic correlation were approximated using formulae described by Funkhouser and Grossman (1982) and Grossman (1970, 1974), respectively. Estimates of phenotypic correlations were also obtained; their standard errors were assessed from the variance among estimates in different replicates.

Regressions of offspring on sire, dam (intra-sire) or mid-parent values were calculated for each pair of generations (1–0, 2–1, 3–2) and pooled across pairs; this was done separately for each replicate. Heritability was estimated as twice the offspring-parent regression, or directly from the regressions of offspring on mid-parent. Unweighted means of heritability estimates were calculated, and the standard errors of these means were computed using the variance between estimates in the five replicates.

Assortative mating group

With assortative mating, assumptions made regarding (4) do not hold because within a mating pair, sire and dam effects become correlated through their phenotypic values. Assortative mating for trait X leads to

$$\mathrm{Cov}(s^X, d^Y) = \tfrac{1}{4}\,\mathrm{Cov}_A^{XY}\,\varrho\, h_x^2 \qquad (6)$$

where s^X and d^Y are transmitting abilities of sires and dams for traits X and Y, respectively, Cov_A^{XY} is the additive genetic covariance between X and Y, and h_X^2 is the heritability of trait X (Gianola 1982). Assortative mating complicates the expected values of correlations between relatives, as shown in Table 1.

Table 1. Expected value of correlations between relatives for traits X, Y and Z under assortative mating for X (after Gianola 1982)

Correlation	Expected value[a]
A. Offspring-parent	
1. (X, X)	$h_X^2(1+\varrho)/2$
2. (X, Y)	$(\theta_{XY} h_X h_Y + h_X^2 \varrho r_{XY})/2$
3. (Y, X)	$\theta_{XY} h_X h_Y (1+\varrho)/2$
4. (Y, Y)	$h_Y^2(1+\theta_{XY}^2 \varrho h_X^2)/2$
5. (X, Z)	$(\theta_{XZ} h_X h_Z + h_X^2 \varrho r_{XZ})/2$
6. (Z, X)	$\theta_{XZ} h_X h_Z (1+\varrho)/2$
7. (Z, Z)	$h_Z^2(1+\theta_{XZ}^2 \varrho h_X^2)/2$
8. (Z, Y)	$\theta_{ZY} h_Z h_Y (1+\theta_{XY}\theta_{XZ} \varrho h_X^2)/2$
B. Full-sibs	
9. (X, X)	$h_X^2(1+\varrho h_X^2)/2 + d_X^2/4 + m_X^2$
10. (X, Y)	$\theta_{XY} h_X h_Y (1+\varrho h_X^2)/2 + r_{d_{XY}} d_X d_Y/4$ $+ r_{m_{XY}} m_X m_Y$
11. (Y, Y)	$h_Y^2(1+\theta_{XY}^2 \varrho h_X^2)/2 + d_Y^2/4 + m_Y^2$
12. (X, Z)	$\theta_{XZ} h_X h_Z (1+\varrho h_X^2)/2 + r_{d_{XZ}} d_X d_Z/4$ $+ r_{m_{XZ}} m_X m_Z$
13. (Z, Z)	$h_Z^2(1+\theta_{XZ}^2 \varrho h_X^2)/2 + d_Z^2/4 + m_Z^2$
14. (Z, Y)	$\theta_{ZY} h_Z h_Y (1+\theta_{XY}\theta_{XZ} \varrho h_X^2)/2 + r_{d_{ZY}} d_Z d_Y/4$ $+ r_{m_{ZY}} m_Z m_Y$
C. Half-sibs	
15. (X, X)	$h_X^2[1+h_X^2 \varrho(2+\varrho)]/4$
16. (X, Y)	$\theta_{XY} h_X h_Y [1+h_X^2 \varrho(2+\varrho)]/4$
17. (Y, Y)	$h_Y^2[1+\theta_{XY}^2 h_X^2 \varrho(2+\varrho)]/4$
18. (X, Z)	$\theta_{XZ} h_X h_Z [1+h_X^2(2+\varrho)]/4$
19. (Z, Z)	$h_Z^2[1+\theta_{XZ}^2 h_X^2 \varrho(2+\varrho)]/4$
20. (Z, Y)	$\theta_{ZY} h_Z h_Y [1+\theta_{XY}\theta_{XZ} h_Y^2 \varrho(2+\varrho)]/4$

[a] h_X^2, h_Y^2, h_Z^2 are equilibrium heritabilities; θ_{XY}, θ_{XZ}, θ_{ZY} are equilibrium genetic correlations; r_{XY} and r_{XZ} are equilibrium phenotypic correlations; d_X^2, d_Y^2, d_Z^2 are relative contributions of dominance to variance; $r_{d_{XY}}$, $r_{d_{XZ}}$, $r_{d_{ZY}}$ are correlations between dominance deviations; m_X^2, m_Y^2, m_Z^2 are maternal contributions to variance; $r_{m_{XY}}$, $r_{m_{XZ}}$, $r_{m_{ZY}}$ are correlations between maternal deviations; ϱ is phenotypic correlation between mates

At generation 3, the A population was expected to be "close" to equilibrium (Crow and Kimura 1970; Bulmer 1980). Offspring-parent correlations within the A group were calculated separately for each replicate using data from generations 2 and 3. Also, within each replicate, individuals in a half-sib or full-sib family were paired as described by Mwenya (1983), and correlations between sibs were calculated using product-moment techniques.

Let $\mathbf{y}_i$ be the 20×1 vector of calculated correlations between relatives (Table 1) in the replicate i (i = 1, ..., 5). Put

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \mathbf{y}_3 \\ \mathbf{y}_4 \\ \mathbf{y}_5 \end{bmatrix} = \begin{bmatrix} \mathbf{f}(\boldsymbol{\psi}) \\ \mathbf{f}(\boldsymbol{\psi}) \\ \mathbf{f}(\boldsymbol{\psi}) \\ \mathbf{f}(\boldsymbol{\psi}) \\ \mathbf{f}(\boldsymbol{\psi}) \end{bmatrix} + \begin{bmatrix} \boldsymbol{\varepsilon}_1 \\ \boldsymbol{\varepsilon}_2 \\ \boldsymbol{\varepsilon}_3 \\ \boldsymbol{\varepsilon}_4 \\ \boldsymbol{\varepsilon}_5 \end{bmatrix} \qquad (7)$$

where $E(\mathbf{y}_i) = \mathbf{f}(\boldsymbol{\psi})$ is a vector of non-linear functions of the parameter vector whose components are defined in Table 1:

$$\begin{aligned}\boldsymbol{\psi}' = [&h_X, h_Y, h_Z, \theta_{XY}, \theta_{XZ}, \theta_{YZ}, d_X, d_Y, d_Z, r_{d_{XY}}, r_{d_{XZ}}, r_{d_{YZ}},\\ &m_X, m_Y, m_Z, r_{m_{XY}}, r_{m_{XZ}}, r_{m_{YZ}}, r_{XY}, r_{XZ}]\end{aligned} \qquad (8)$$

where X, Y and Z stand for pupal weight, larval weight and pupation time, respectively. Note that $\boldsymbol{\psi}$ contains as many parameters as correlations in replicate i; thus, $\boldsymbol{\psi}$ was reduced eventually. Additional assumptions were $\boldsymbol{\varepsilon}_i \sim (\mathbf{0}, \boldsymbol{\Sigma}_i)$, and $\mathrm{Cov}(\boldsymbol{\varepsilon}_i, \boldsymbol{\varepsilon}_j') = 0$. The matrix $\boldsymbol{\Sigma}_i$ is not diagonal as it contains theoretical covariances between the 20 correlations calculated from the same data in replicate i. Because these covariances are difficult to obtain analytically, $\boldsymbol{\Sigma}_i$ was approximated as $\mathbf{V}_i$, a diagonal matrix containing estimates of the diagonal elements of $\boldsymbol{\Sigma}_i$; calculation of the elements of $\mathbf{V}_i$ is described later.

The estimate of $\boldsymbol{\psi}$ was obtained by minimizing

$$S = [\mathbf{y} - \mathbf{f}]'\, \mathbf{V}^{-1} [\mathbf{y} - \mathbf{f}] \qquad (9)$$

with respect to $\boldsymbol{\psi}$, where $\mathbf{y}' = [\mathbf{y}_1', \ldots, \mathbf{y}_5']$, $\mathbf{f}' = [\mathbf{f}'(\boldsymbol{\psi}), \ldots, \mathbf{f}'(\boldsymbol{\psi})]$, and

$$\mathbf{V}^{-1} = + \mathbf{V}_i^{-1}$$

is a direct-sum operation over the matrices indicated (Searle 1982). Now

$$\frac{\partial S}{\partial \boldsymbol{\psi}} = \frac{\partial \mathbf{f}'}{\partial \boldsymbol{\psi}} \cdot \frac{\partial S}{\partial \mathbf{f}} = -2\,\mathbf{K}'\,\mathbf{V}^{-1} [\mathbf{y} - \mathbf{f}] \qquad (10)$$

where $\mathbf{K}'$ is a matrix containing first derivatives of $\mathbf{f}'$ with respect to $\boldsymbol{\psi}$. Expansion of $\mathbf{f}(\boldsymbol{\psi})$ with a first order Taylor series about the starting vector $\boldsymbol{\psi}^0$ gives

$$\mathbf{f}(\boldsymbol{\psi}) = \mathbf{f}(\boldsymbol{\psi}^0) + \mathbf{K}_0'(\boldsymbol{\psi} - \boldsymbol{\psi}^0) \qquad (11)$$

where $\mathbf{K}_0$ is $\mathbf{K}$ evaluated at $\boldsymbol{\psi}^0$. Using (11) in (10), setting to $\mathbf{0}$ and rearranging yields a sequence of iterations

$$\boldsymbol{\psi}^{l} = \boldsymbol{\psi}^{l-1} + [\mathbf{K}_{l-1}'\,\mathbf{V}_{l-1}^{-1}\,\mathbf{K}_{l-1}]^{-1}\,\mathbf{K}_{l-1}\,\mathbf{V}_{l-1}^{-1}[\mathbf{y} - \mathbf{f}(\boldsymbol{\psi}^{l-1})]$$

where $\boldsymbol{\psi}^l$ is a solution at the literate l, and $\mathbf{K}_{l-1}'$ and $\mathbf{V}_{l-1}^{-1}$ are $\mathbf{K}'$ and $\mathbf{V}^{-1}$ evaluated at iterate $l-1$. The computations were carried out with the NLIN procedure of SAS (SAS Institute 1982), using the technique of segmented models.

The matrix $\mathbf{V}_i^{-1}$ was calculated and recalculated at each iterate ($l = 0, 1 \ldots$) following Eaves (1975), as

$$\mathbf{V}_i^{-1} = \mathrm{Diag}\,\frac{n_{ij} - 2}{[1 - f_{ij}^2(\boldsymbol{\psi}^l)]^2}\,, \qquad (12)$$

where $f_{ij}(\boldsymbol{\psi}^l)$ is an estimate of $f_{ij}(\boldsymbol{\psi})$, the expected value of correlation j in replicate i (i = 1, ..., 5; j = 1, ..., 20), and n_{ij} is the number of pairs used in calculating the correlation. To ascertain whether convergence to a global minimum had occurred, different sets of trial values were used for iteration.

During iteration, elements of ψ were kept within the parameter space:

$$0 \leqq (h_X, h_Y, h_Z, d_X, d_Y, d_Z, m_X, m_Y, m_Z) \leqq 1$$

and

$$-1 \leqq (\theta_{XY}, \theta_{XZ}, \theta_{YZ}, r_{d_{XY}}, r_{d_{XZ}}, r_{d_{YZ}}, r_{m_{XY}}, r_{m_{XZ}}, r_{m_{YZ}}, r_{XY}, r_{XZ}) \leqq 1 .$$

Iteration ended when $\| \psi^l - \psi^{l-1} \| / 20 < 10^{-8}$. The variance-covariance matrix of the estimates was estimated as

$$\hat{\mathrm{V}}\mathrm{ar}(\hat{\psi}) = [\mathbf{K}' \, \mathbf{V}^{-1} \, \mathbf{K}]^{-1}_{\psi = \hat{\psi}} \tag{13}$$

where $\hat{\psi}$ is the value of ψ which minimizes (9).

The procedure was repeated using z-transforms of elements of $\mathbf{y}$ to obtain a better approximation to normality and to render $\mathbf{V}$ less dependent on ψ. With y_{ij} being correlation j in replicate i, we calculated

$$z_{ij} = \frac{1}{2} \ln \left[\frac{1 + y_{ij}}{1 - y_{ij}} \right] . \tag{14}$$

Following Fisher (1921)

$$E(z_{ij}) = \frac{1}{2} \ln \left[\frac{1 + f_{ij}(\psi)}{1 - f_{ij}(\psi)} \right] = \mu_{ij} \tag{15}$$

and

$$\mathrm{Var}(z_{ij}) = 1/n_{ij} . \tag{16}$$

The parameter vector ψ was estimated as before by minimizing

$$Q = (\mathbf{z} - \boldsymbol{\mu})' \, \mathbf{N} \, (\mathbf{z} - \boldsymbol{\mu}) \tag{17}$$

with respect to ψ, where $\mathbf{z}$ is a vector of z_{ij}'s, $\boldsymbol{\mu}$ is a vector of μ_{ij}'s and $\mathbf{N} = \mathrm{diag}\,\{n_{ij}\}$.

Results and discussion

Estimates of genetic parameters in the randomly mated group

Heritabilities and genetic and phenotypic correlations estimated in the randomly mated group (R) using model (4) are in Tables 2 and 3. Heritabilities (Table 2) were within the range of those reported in studies involving the same foundation strain (Yamada and Bell 1969; Scheinberg et al. 1967; Bell and Moore 1972). Heritabilities based on sire component of variance were smaller for all traits than those obtained from the dam component. This difference, more pronounced for larval weight than for other traits, could be due to dominance or maternal effects. These effects have been reported to affect larval weight (King and Dawson 1972) and pupal weight (Bondari et al. 1978). Yamada and Bell (1969) argued that larger estimates from the dam component of variance might be due to dominance rather than to maternal effects.

Genetic and phenotypic correlations (Table 3) were generally in agreement with previous studies conducted in the same foundation stock (Bell 1969; Bell and More 1972; Englert and Bell 1969, 1970). In our study, the genetic correlation between PW and LW in the R-mated population was negative (– 0.21 ± 0.23) when estimated from the sire component of covariance, but positive (0.10 ± 0.19) using the dam component. While this might reflect the large sampling variance of the estimates, perhaps additive, dominance and maternal effects contribute to the covariance between these two traits in opposite directions. The genetic correlation between PW and PT was positive in the present research and those from sire and dam components were in agreement. However, studies using the same stock (Bell 1969; Bell and Burris 1973) yielded negative genetic correlations between these two traits. Nevertheless, Englert and Bell (1970) have reported positive genetic correlations between PW and PT in some related populations. Further, Howe (1961) demonstrated the dependence of the sign and magnitude of the genetic correlation between PW and PT on the frequencies of "quick" and "slow" developing individuals in the population. When one type was more frequent than the other, the correlation was high and negative; the opposite was true when their frequencies were about equal (Howe 1961). In the present study, frequencies of the above two types were perhaps equal.

There was little or no difference between regressions of sons on sires and of daughters on sires. The same was true with regressions of sons on dams (intra-sires) and of daughters on dams (intra-sires). Hence,

Table 2. Heritabilities ± SE obtained from sib covariances in the randomly mated group

Estimate[b]	Trait[a]		
	PW	LW	PT
$\hat{h}^2_s$	0.30 ± 0.12	0.26 ± 0.14	0.39 ± 0.10
$\hat{h}^2_d$	0.48 ± 0.17	0.93 ± 0.18	0.44 ± 0.15
$\hat{h}^2_{s+d}$	0.39 ± 0.15	0.59 ± 0.16	0.39 ± 0.09

[a] PW: pupal weight; LW: larval weight; PT: pupation time
[b] $\hat{h}^2_s$, $\hat{h}^2_d$ and $\hat{h}^2_{s+d}$ are heritability estimates obtained from sire, dam and sire plus dam components of variance

Table 3. Genetic (r_g) and phenotpyic (r_p) correlations ± SE obtained using sib covariances in the randomly mated group

Estimate[a]	Traits[b]		
	PW and LW	PW and PT	LW and PT
$\hat{r}_{g_s}$	– 0.21 ± 0.23	0.45 ± 0.10	– 0.77 ± 0.10
$\hat{r}_{g_d}$	0.10 ± 0.19	0.43 ± 0.41	– 0.72 ± 0.40
$\hat{r}_{g_{s+d}}$	– 0.15 ± 0.09	0.44 ± 0.16	– 0.71 ± 0.35
$\hat{r}_p$	– 0.17 ± 0.21	0.49 ± 0.22	– 0.69 ± 0.25

[a] s, d and s + d indicate estimates obtained from sire, dam, and sire plus dams components of variance and covariance
[b] PW: pupal weight; LW: larval weight; PT: pupation time

Table 4. Heritabilities ± SE obtained from regression of offspring on sire ($\hat{h}^2_{os}$) and on dam (intra-sire) ($\hat{h}^2_{od}$), and of offspring on mid-parent ($\hat{h}^2_{om}$) in the randomly mated group

Estimate	Trait[a]		
	PW	LW	PT
$\hat{h}^2_{os}$	0.31 ± 0.08	0.09 ± 0.04	0.17 ± 0.03
$\hat{h}^2_{od}$	0.36 ± 0.08	0.14 ± 0.08	0.09 ± 0.11
$\hat{h}^2_{om}$	0.34 ± 0.02	0.15 ± 0.02	0.16 ± 0.02

[a] PW: pupal weight; LW: larval weight; PT: pupation time

only regressions of offspring on parents will be reported here. Heritabilities based on these regressions in the R-mated group are in Table 4. There were small differences between heritabilities obtained from the three regressions. Heritabilities of PW were similar to the one obtained from covariance between half-sibs (0.30±0.12, Table 2). However, heritabilities for LW and PT were smaller than their half-sib counterparts in Table 2. This suggests a negative covariance between additive direct and genetic maternal effects affecting these traits (Willham 1963).

Estimates of genetic parameters in the assortatively mated group

The average value of the correlation between pupal weights of mates was 0.98. In the A-mated group, the iterative procedure failed to converge when the parameter vector ψ was as in (8). Dominance and maternal contributions and associated correlations were then deleted from the model but the procedure still did not converge. Further modifications of the model were made: a) correlations with expected values being a function of more than 5 parameters (e.g., offspring-parent correlation between Z−Y values: see Table 1) were deleted from the analysis so the parameter vector became $\psi' = [h_X, h_Y, h_Z, \theta_{XY}, \theta_{XZ}, r_{XY}, r_{XZ}]$; and b) the restriction was lifted that estimates of parameters had to be within the parameter space during iteration. Using estimates of genetic parameters from the R-mated group (with genetic correlations set to zero) as starting values, the procedure converged in 7 and 4 iterations for raw and z-transformed correlations, respectively. The iterative procedure also converged to the same values when different starting sets were used. Results of the iteration for a particular set of starting values are in Tables 5 and 6 for the analyses with raw and z-transformed correlations, respectively. Estimates of parameters were essentially the same in both cases. Only the estimate of phenotypic correlation between PW and PT was outside the parameter space. The estimate of genetic correlation between LW and PT could not be obtained in the A-mated group because this parameter had to be dropped from the model.

Table 5. Assortatively mated group: values of the parameters during iteration (analysis with raw correlations)

Parameter[a]	Iteration			
	0	3	5	7
h_X	0.5100	0.6264	0.6264	0.6264
h_Y	0.6000	0.6889	0.6888	0.6888
h_Z	0.5100	0.4951	0.4951	0.4951
θ_{XY}	0	0.2718	0.2721	0.2721
θ_{XZ}	0	0.1457	0.1457	0.1457
r_{XY}	−0.0100	−0.2353	−0.2355	−0.2355
r_{XZ}	0.5400	1.0138	1.0138	1.0138

[a] X: pupal weight; Y: larval weight; Z: pupation time
See footnote to Table 1 for definition of the parameters

Table 6. Assortatively mated group: values of the parameters during iteration (analysis with z-transformed correlations)

Parameter[a]	Iteration			
	0	2	3	4
h_X	0.5100	0.6394	0.6381	0.6381
h_Y	0.6000	0.7029	0.6956	0.6956
h_Z	0.5100	0.4961	0.4957	0.4957
θ_{XY}	0	0.2696	0.2620	0.2620
θ_{XZ}	0	0.1444	0.1432	0.1432
r_{XY}	−0.0100	−0.2359	−0.2215	−0.2215
r_{XZ}	0.5400	1.0686	1.0508	1.0508

[a] X: pupal weight; Y: larval weight; Z: pupation time
See footnote to Table 1 for definition of the parameters

Estimates of parameters in the R-mated and A-mated groups, with their approximate standard errors, are in Table 7. Heritabilities were larger in the A-mated group for PW and LW, but not for PT. The increase in heritability was higher for LW (88%) than for PW (30%), the trait on which mating was assortative. The increase in heritability of PW was in agreement with theory because assortative mating for a trait with h^2 ranging, say, from 0.26 to 0.30 would be expected to yield an equilibrium heritability between 0.35 and 0.42 after assortative mating with $\varrho = 0.98$ (Bulmer 1980). The standard errors of heritabilities were lower in the A-group because the variance-covariance matrix of estimates depends on the number of pairs formed, as shown in equations (12) and (13). Because the information in each pair was treated as being statistically independent of that contributed by another pair, the standard errors calculated with (13) would tend to understate the "true" sampling variance of estimates.

Table 7. Summary of estimates of parameters ± SE in randomly mated (R) and assortatively mated (A) groups

Parameter[a]	Group	
	R[b]	A[c]
h^2_X	0.30 ± 0.12	0.39 ± 0.02 (0.41 ± 0.02)
h^2_Y	0.26 ± 0.13	0.49 ± 0.04 (0.48 ± 0.05)
h^2_Z	0.39 ± 0.10	0.25 ± 0.03 (0.25 ± 0.03)
θ_{XY}	−0.21 ± 0.23	0.27 ± 0.10 (0.26 ± 0.09)
θ_{XZ}	0.45 ± 0.10	0.15 ± 0.14 (0.14 ± 0.12)
θ_{YZ}	−0.77 ± 0.14	not estimable
r_{XY}	−0.17 ± 0.21	−0.24 ± 0.38(−0.22 ± 0.33)
r_{XZ}	0.49 ± 0.22	1.01 ± 0.32 (1.05 ± 0.34)
r_{YZ}	−0.69 ± 0.25	not estimable

[a] See Table 1 for definition of parameters. X: pupal weight; Y: larval weight; Z: pupation time

[b] Entries are half-sib estimates (in parentheses)

[c] Entries are estimates from raw and z-transformed correlations (in parentheses)

The genetic correlation between PW and LW in the R-mated group was negative, but those in the A-mated group were positive. Aside from possible differences due to sampling variability, this is inconsistent with Gianola (1982) who found that positive assortative mating for trait X should decrease a negative genetic correlation between X and Y in random mating. The genetic correlation between PW and PT was also decreased by assortative mating, which is also in conflict with Gianola (1982). However, as pointed out before, a positive genetic correlation between PW and PT in random mating is also in conflict with other studies (Bell 1969; Bell and Burris 1973).

Within full-sib family variances of pupal weight (grams squared) in R and A groups were 0.048 (R) and 0.047 (A) in generation 1; 0.054 (R) and 0.041 (A) in generation 2; and 0.050 (R) and 0.046 (A) in generation 3. Estimates in the A group tended to be smaller than those in the R group. Breese (1956) showed that in the absence of dominance, assortative mating increased variance among family means but did not affect genetic variance within families. With dominance and a large number of loci affecting the trait, within-family genetic variance was also unaffected by assortative mating. However, Rao and Narain (1967) showed with a single locus model that with dominance the genetic variance following assortative mating tends to concentrate in the variance among family means. The reduction in within-family variance observed in this study suggests that non-additive gene action in a few number of segregating loci cannot be discounted.

In conclusion, this study supports the theory that assortative mating of parents without selection can increase the heritability of a quantitative trait. Effects of assortative mating on the genetic covariance structure were not as expected from theory, although the results observed may be due to sampling variation. To investigate this point, further experimentation on a larger scale would be needed.

References

Bell AE (1969) The nature of selection responses in *Tribolium.* Jpn J Genet (Supp 1) 44:299–309

Bell AE, Burris MJ (1973) Simultaneous selection for two correlated traits in *Tribolium.* Genet Res 21:29–46

Bell AE, Moore CH (1972) Reciprocal recurrent selection for pupal weight in Tribolium in comparison with conventional methods. Egypt J Genet Cytol 1:92–119

Bondari K, Willham RL, Freeman AE (1978) Estimates of direct and maternal genetic correlations for pupa weight and family size of Tribolium. J Anim Sci 47:358–365

Breese EL (1956) The genetical consequences of assortative mating. Heredity 10:323–343

Bulmer MG (1980) The mathematical theory of quantitative genetics. Clarendon Press, Oxford

Crow JF, Felsenstein J (1968) The effect of assortative mating on the genetic composition of a population. Eugen Q 15:85–97

Crow JF, Kimura M (1970) An introduction to population genetics theory. Harper and Row, New York

Eaves LJ (1975) Testing models for variation in intelligence. Heredity 34:132–136

Englert DC, Bell AE (1969) Components of growth in genetically diverse populations of *Tribolium castaneum.* Can J Genet Cytol 11:896–907

Englert DC, Bell AE (1970) Selection for time of pupation in *Tribolium castaneum.* Genetics 64: 541–552

Felsenstein J (1981) Continuous-genotype models and assortative mating. Theor Popul Biol 19:341–357

Fernando RL, Gianola D (1984) Rules for assortative mating in relation to selection for linear merit functions. Theor Appl Genet 68:227–237

Fisher RA (1921) On the "probable error" of a coefficient of correlation deduced from a small sample. Metron 1:3–37

Funkhouser EM, Grossman M (1982) Bias in estimation of the sampling variance of an estimate of heritability. J. Hered 73:139–141

Gianola D (1982) Assortative mating and the genetic correlation. Theor Appl Genet 62:225–231

Grossman M (1970) Sampling variance of the correlation coefficients estimated from analysis of variance and covariance. Theor Appl Genet 40:357–359

Grossman M, Norton HW (1974) Simplification of the sampling variance of the correlation coefficients. Theor Appl Genet 44:332

Howe RW (1961) Developmental time and weight in *Tribolium castaneum.* Tribol Inf Bull 4:21–22

King CE, Dawson PS (1972) Population biology in the *Tribolium* model. Evol Biol 5:133–227

Latter BDH (1965) Quantitative genetic analysis in *Phalaris tuberosa.* 1. The statistical theory of open pollinated progenies. Genet Res 6:51–60

Mwenya WNM (1983) Response to selection for pupal weight with and without assortative mating in *Tribolium castaneum.* PhD Thesis, University of Illinois

Rao AV, Narain P (1967) Genetic variance and assortative mating. J Indian Soc Agric Stat 19: 32–45

Reeve ECR (1953) Studies in quantitative inheritance. 3. Heritability and genetic correlation in progeny tests using different mating systems. J Genet 51: 529–542

Reeve ECR (1961) A note on nonrandom mating in progeny tests. Genet Res 2: 195–203

SAS (1982) SAS User's Guide. Statistical Analysis System Institute Inc, Cary NC

Scheinberg E, Bell AE, Anderson VL (1967) Genetic gains in populations of *Tribolium castaneum* under uni-stage tandem selection and under restricted selection indices. Genetics 55:69–90

Searle SR (1982) Matrix algebra useful for statistics. Wiley and Sons, New York

Van Vleck LD, Hudson GFS (1982) Relationships among sires in estimating genetic variance. J Dairy Sci 65: 1663–1665

Vetta A (1976) Correction to Fisher's correlations between relatives and environmental effects. Nature 263: 316–317

Willham RL (1963) The covariance between relatives for characters composed of components contributed by related individuals. Biometrics 19: 18–27

Yamada Y, Bell AE (1969) Selection for larval growth in *Tribolium* under two levels of nutrition. Genet Res 13: 175–195