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The joint effects of selection and assortative mating on multiple polygenic characters

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Introduction and notation

In the companion paper (Tallis and Leppard 1988) (T & L), the joint effects of selection and assortative mating on a single polygenic character were examined. It is the purpose of this paper to extend the results to multiple characters.

The same structure and notation will be used as in T & L, with the exception that the treatment allow for $q \geqq 1$ characters. It is assumed that selection and assortative mating, which is abbreviated to "assortation", are with respect to a linear combination of the characters. The notation of the scalar case carries over if the random variables p and g are interpreted as q-dimensional random vectors, P and G being $(q \times q)$ covariance matrices. The generalisation of h^2 is $H = G P^{-1}$ and with these modifications, equation (4) of T & L becomes:

$$g_{n+1} = \frac{H_n}{2} (p_{n1} + p_{n2}) \delta_n \tag{1}$$

where $V[\delta_n] = \frac{1}{2} (G_0 + G_n - H_n P_n H_n')$, the covariance matrix of δ_n.

In a manner yet to be specified, under selection P_n changes to P_{sn1} in the male population and P_{sn2} in the female population, where:

$$P_{snj} = (I + K_{nj}) P_n, \quad K_{nj} = (P_{snj} - P_n) P_n^{-1}, \quad j = 1, 2.$$

Further, under assortation a covariance term $C[p_{n1}, p_{n2}] = C_n(p) = E[p_{n1} p_{n2}]$ is induced, where C stands for covariance, so that:

$$V[p_{n1} + p_{n2}] = 2 P_n + 2 [\bar{K}_n P_n + \bar{C}_n]$$

where $V[x] = C[x, x]$, $\bar{K}_n = \frac{1}{2} [K_{n1} + K_{n2}]$ and $\bar{C}_n = \frac{1}{2} (C_n(p) + C_n'(p))$.

Using this result:

$$V[g_{n+1}] = G_{n+1} = \frac{G_n}{2} + \frac{G_0}{2} + \frac{1}{2} H_n (\bar{K}_n P_n + \bar{C}_n) H_n' \tag{2}$$

so that, subtracting G_0 from both sides,

$$D_{n+1} = \frac{D_n}{2} + \frac{1}{2} H_n (\bar{K}_n P_n + \bar{C}_n) H_n' = \sum_{i=0}^{n} 2^{-(n+1-i)} H_i (\bar{K}_i P_i + \bar{C}_i) H_i' \tag{3}$$

where $D_n = G_n - G_0$ is the "disequilibrium" component of the covariance matrix G_n. Provided K_i tends to a limit matrix $\bar{K}$, the equilibrium equation is:

$$\hat{D} = \hat{H} (\bar{K} \hat{P} + \hat{\bar{C}}) \hat{H}'. \tag{4}$$

It is assumed that selection is such that $\bar{K}$ is well defined.

The form of $\bar{K}_n$ and $\bar{C}_n(p)$

In order to carry out the processes of selection and assortation we introduce indices $I_n = \beta_n' p_n$ and $A_n = b_n' p_n$. The choice of β_n and b_n is left open, although one could mostly expect:

$$\beta_n = b_n = P_n^{-1} G_n w$$

where w is a vector of economic weights for the q characters. This corresponds to using the usual selection index for both processes.

However, various special cases can also be covered by, for instance, taking a component of β_n equal to unity and the rest zero. This corresponds to selection for a single character, and b_n can be chosen to conform with β_n, or else it can be set to allow assortation to take place on a character different to the one used for selection.

In any case, the covariance matrix for I_n, A_n and p_n is:

$$V_n = \begin{bmatrix} V[I_n] & C[I_n, A_n] & L'[I_n] \\ C[I_n, A_n] & V[A_n] & L'[A_n] \\ L[I_n] & L[A_n] & P_n \end{bmatrix}. \quad (5)$$

Note that $V[I_n] = \beta_n' P_n \beta_n$, $C[I_n, A_n] = \beta_n' P_n b_n$, $L[I_n] = P_n \beta_n$ and $L[A_n] = P_n b_n$, so that V_n is well defined in terms of the basic parameters.

Under selection, $V[I_n]$ becomes $(1 + k_j) V[I_n] = V_{sj}[I_n]$, $j = 1, 2$, for the two sexes and this leads to an adjustment in the covariance matrix for A_n and p_n as follows a direct application of equation (8) of Tallis (1987):

$$\begin{bmatrix} V_{sj}[A_n] & L_{sj}'[A_n] \\ L_{sj}[A_n] & P_{sjn} \end{bmatrix} = \begin{bmatrix} V[A_n] & L'[A_n] \\ L[A_n] & P_n \end{bmatrix} + [V[I_n]]^{-1} k_j \begin{bmatrix} C[I_n, A_n] \\ L[I_n] \end{bmatrix} [C[I_n, A_n]\, L[I_n]] \quad (6)$$

From (6), P_{sjn} can be obtained directly, as can $L_{sj}[A_n]$. Once P_{sjn} is found, K_{nj} and $\bar{K}_n$ can be constructed.

The calculation of $C_n(p)$ requires the mating transfer system (M.T.S.), for index assortation, viz.

$\{g_{n1}, p_{n1}, A_{n1}, A_{n2}, p_{n2}, g_{n2}\}$,

(see Tallis 1985, Section 7). Using the properties of multidimensional transfer systems given in that paper:

$$C_n(p) = C[p_{n1}, p_{n2}] = m_A [V_{s1}[A_n] V_{s2}[A_n]]^{-\frac{1}{2}} L_{s1}[A_n] L_{s2}[A_n]' \quad (7)$$

where m_A is the correlation between the A_n values of mates. Since $2\bar{C}_n(p) = C_n(p) + C_n'(p)$, all the ingredients are available to recursively calculate D_n, $G_n = G_0 + D_n$ and $P_n = P_0 + D_n$.

The vector of selection differentials for the q characters is given by

$$\Delta_n = H_n L(I_n) [V[I_n]]^{-\frac{1}{2}} \bar{\tau} \quad (8)$$

where $\bar{\tau}$ is as defined in T & L (12).

The performance of the index I_n in relation to economic genotype $w' g_n$ is specified by the expected genetic gain for I_n, $w' \Delta_n$.

It is possible to argue that $b_n = \beta_n$ is an appropriate choice. Put $t_n = w' g_n$, then the model for t_{n+1} is:

$$t_{n+1} = \frac{w' H_n}{2} (p_{n1} + p_{n2}) + w' \delta_n$$

and

$$V[t_{n+1} \mid m_A] - V[t_{n+1} \mid m_A = 0] = \tfrac{1}{2} w' H_n \bar{C}_n H_n' w.$$

tion. Thus, dropping the subscript n, we wish to maximise $w' H \bar{C}(p) H' w$, where

$$2\bar{C}(p) = C(p) + C'(p),$$
$$C(p) = m_A [V[A]]^{-1} L[A] L'[A]$$
$$L[A] = E[p, p' b] = P b, \quad V[A] = b' P b.$$

Thus

$$\bar{C}(p) = \frac{m_A}{b' P b} P b b' P$$

and it is required to maximise

$$(w' G b)^2 / b' P b.$$

The solution is found immediately from Rao (1965, p 48 1 f. 1.1) as

$$b = P^{-1} G w = \beta. \quad (9)$$

Covariance between relatives

The covariances between relatives are calculated in a similar way so that used in T & L. In particular, the pedigrees are identical and will not be repeated here.

Put $\hat{P} = P_0 + \hat{D}$, $\hat{G} = G_0 + \hat{D}$, $\hat{H} = \hat{G} \hat{P}^{-1}$ and construct the equilibrium form of (6) using $\hat{P}$ and $\hat{G}$. This defines $\hat{V}_{sj}[A]$, $\hat{L}_{sj}[A]$ and $\hat{P}_{sj}$, so that $\hat{K}_j = (\hat{P}_{sj} - \hat{P}) \hat{P}^{-1}$.

In order to find $\hat{G}_{sj}$, $\hat{C}(p)$ and $\hat{C}(g)$, use is made of the equilibrium M.T.S. $\{g_1, p_1, A_1, A_2, p_2, g_2\}$ and the model $g = \hat{H} p + \varepsilon$, $V[\varepsilon] = \hat{G} - \hat{H} \hat{P} \hat{H}'$, $C[p, \varepsilon] = 0$. Now, as a result of selection $V_s[g_j] = \hat{G}_{sj} = \hat{H} \hat{P}_{sj} \hat{H}'$ and the covariance between g_j and p_j is $C_s[g_j, p_j] = \hat{H} \hat{P}_{sj}$. Hence,

$$\hat{C}(p) = m_A [\hat{V}_{s1}[A] \hat{V}_{s2}[A]]^{-\frac{1}{2}} \hat{L}_{s1}[A] \hat{L}_{s2}[A]' \quad \text{and}$$
$$\hat{C}(g) = \hat{H} \hat{C}(p) \hat{H}'.$$

Full-sibs

Although the calculations are similar to those of the single character case, there are sufficient differences to justify some repetition. If the pedigree transfer system is abbreviated to P.T.S. (Tallis and Leppard 1988; Tallis 1985) and the rules of multivariate transfer systems are used:

P.T.S. $\{p_{11}, g_{11}, g_{12}, p_{12}\}$

M.T.S. $\{g_{01}, p_{01}, A_{01}, A_{02}, p_{02}, g_{02}\}$

$$\begin{aligned} \hat{C}[S, S] = C[p_{11}, p_{12}] &= C[p_{11}, g_{11}] [V[g_{11}]]^{-1} C[g_{11}, g_{12}] \\ &\cdot [V[g_{12}]]^{-1} C[g_{12}, p_{12}] \\ &= \hat{G} \hat{G}^{-1} C[\tfrac{1}{2}(g_{01} + g_{02}), \quad (10) \end{aligned}$$

[illegible]

Parent-offspring

P.T.S. $\{p_{01}, g_{11}, p_{11}\}$

M.T.S. $\{g_{01}, p_{01}, A_{01}, A_{02}, p_{02}, g_{02}\}$

$$\begin{aligned}\hat{C}[P,0] &= C[p_{01}, g_{11}]\,[V[g_{11}]]^{-1}\,C[g_{11}, p_{11}] \\ &= C[p_{01}, \tfrac{1}{2}(g_{01}+g_{02})] \\ &= \tfrac{1}{2}\hat{P}_1\hat{H}' + \tfrac{1}{2}C[p_{01}, g_{02}] \\ &= \tfrac{1}{2}(\hat{P}_1 + \hat{C}(p))\,\hat{H}'. \qquad (11)\end{aligned}$$

Half-sibs

P.T.S. $\{p_{11}, g_{11}, g_{12}, p_{12}\}$;

M.T.S. $\{g_{01}, p_{01}, A_{01}, A_{02}, A_{03}, p_{03}, g_{03}\}$

$\{g_{01}, p_{01}, A_{01}, A_{02}, p_{02}, g_{02}\}$

$\{g_{02}, p_{02}, A_{02}, A_{03}, p_{03}, g_{03}\}$

$$\begin{aligned}\hat{C}[\tfrac{1}{2}S, \tfrac{1}{2}S] &= C[p_{11}, p_{12}] = \hat{G}\hat{G}^{-1}C[g_{11}, g_{12}]\,\hat{G}^{-1}\hat{G} \\ &= C[\tfrac{1}{2}(g_{01}+g_{02}), \tfrac{1}{2}(g_{02}+g_{03})] \\ &= \tfrac{1}{4}[C[g_{01}, g_{02}] + C[g_{01}, g_{03}] \\ &\quad + V[g_{02}] + C[g_{02}, g_{03}]] \\ &= \tfrac{1}{4}\Big[\hat{G}_1 + 2\hat{C}(g) \\ &\quad + \frac{m_A^2}{\hat{V}_{s2}[A]}\hat{H}\hat{L}_{s2}[A]\,\hat{L}_{s2}[A]'\,\hat{H}'\Big]. \qquad (12)\end{aligned}$$

The terms in the last expression arise by remembering that in the pedigree, P_{01} and P_{03} are female while P_{02} is male.

Numerical example

As an example we consider two characters for sheep, fleece weight (lbs) X_1 and wool fibre diameter X_2. The latter character is assessed by the number of crimps per inch, and the appropriate mean vector, u, and covariances matrices P and G for Merion sheep (Turner et al. 1959) are approximately:

$$u = \begin{pmatrix} 8 \\ 20 \end{pmatrix} \quad P = \begin{pmatrix} 0.6 & -0.6 \\ -0.6 & 4 \end{pmatrix} \quad G = \begin{pmatrix} 0.2 & -0.4 \\ -0.4 & 2 \end{pmatrix}.$$

We consider various cases, assuming n = 30 procedures equilibrium. Δ_{30} and G_{30} are denoted by $\hat{\Delta}$ and $\hat{G}$. The computer program MSELASS, which was used to obtain these results, is described and listed later. In all examples, the proportion of saved males and females, α_1 and α_2, is 0.2.

a) (i). Selection on X_1, no assortation
Specifications: $\beta' = (1,0)$ and $n_A = 0$

$$\hat{\Delta} = \begin{pmatrix} \hat{\Delta}_1 \\ \hat{\Delta}_2 \end{pmatrix} = \begin{pmatrix} 0.304 \\ \ldots \end{pmatrix} \quad \hat{G} = \begin{pmatrix} 0.163 & -0.326 \\ \ldots & \ldots \end{pmatrix}$$

(ii). Selection and assortation X_1
Specifications: $\beta' = (1,0)$, $m_A = 1$ and $b' = (1,0)$

$$\hat{\Delta} = \begin{pmatrix} \hat{\Delta}_1 \\ \hat{\Delta}_2 \end{pmatrix} = \begin{pmatrix} 0.317 \\ -0.634 \end{pmatrix} \quad \hat{G} = \begin{pmatrix} 0.171 & -0.342 \\ -0.342 & 1.885 \end{pmatrix}.$$

b) Selection on X_1, assortation on X_2
Specifications: $\beta' = (1,0)$, $m_A = 1$ and $b' = (0,1)$

$$\hat{\Delta} = \begin{pmatrix} \hat{\Delta}_1 \\ \hat{\Delta}_2 \end{pmatrix} = \begin{pmatrix} 0.327 \\ -0.914 \end{pmatrix} \quad \hat{G} = \begin{pmatrix} 0.178 & -0.496 \\ -0.496 & 3.934 \end{pmatrix}.$$

Note that (a) (ii) and (b) lead to increases of 4% and 8% respectively in $\hat{\Delta}_1$. The fact that (b) is better than the other two is not surprising when (9) is considered.

c) (i). Selection by index
Specifications: $\beta = P^{-1}Gw$, $w' = (4,1)$ (Dunlop and Young 1960) and $m_A = 0$

$$\hat{\Delta} = \begin{pmatrix} \hat{\Delta}_1 \\ \hat{\Delta}_2 \end{pmatrix} = \begin{pmatrix} 0.159 \\ 0.192 \end{pmatrix} \quad \hat{G} = \begin{pmatrix} 0.190 & -0.412 \\ -0.412 & 1.985 \end{pmatrix}$$

$w_1\hat{\Delta}_1 + w_2\hat{\Delta}_2 = 0.828.$

(ii). Selection and assortation by index
Specifications: $\beta = P^{-1}Gw$, $w' = (4,1)$, $m_A = 1$ and $b = \beta$

$$\hat{\Delta} = \begin{pmatrix} \hat{\Delta}_1 \\ \hat{\Delta}_2 \end{pmatrix} = \begin{pmatrix} 0.164 \\ 0.200 \end{pmatrix} \quad \hat{G} = \begin{pmatrix} 0.192 & -0.409 \\ -0.409 & 1.988 \end{pmatrix}$$

$w_1\hat{\Delta}_1 + w_2\hat{\Delta}_2 = 0.856.$

There is a 3.4% advantage due to assortation in this case.

d) (i). Selection by index
Specifications: $\beta = P^{-1}Gw$, $w' = (1,0)$ and $m_A = 0$
This corresponds to the situation in which X_1 is of economic importance, while X_2 is of no commercial consequence.

$$\hat{\Delta} = \begin{pmatrix} \hat{\Delta}_1 \\ \hat{\Delta}_2 \end{pmatrix}\begin{pmatrix} 0.319 \\ -0.897 \end{pmatrix} \quad \hat{G} = \begin{pmatrix} 0.159 & -0.286 \\ -0.286 & 1.679 \end{pmatrix}.$$

(ii). Selection and assortation by index
Specifications: $\beta = P^{-1}Gw$, $w' = (1,0)$, $m_A = 1$ and $b = \beta$

$$\hat{\Delta} = \begin{pmatrix} \hat{\Delta}_1 \\ \hat{\Delta}_2 \end{pmatrix}\begin{pmatrix} 0.335 \\ -0.948 \end{pmatrix} \quad \hat{G} = \begin{pmatrix} 0.168 & -0.309 \\ -0.309 & 1.742 \end{pmatrix}.$$

Thus, various possibilities for selection for gain in whool weight are specified by (a) (i), (a) (ii), (b), (d) (i), and (d) (ii) giving expectations 0.304, 0.317, 0.327, 0.319 and 0.335 respectively. It is clear that introducing the extra character X_2 and using index selection and assortation leads to an increase in expected gain of about 10% (i.e. 0.031/0.304 × 100). This is considerably single character X_1 when assortation leads to an increase of about 4% ($0.013/0.304 \times 100$).

Discussion

In this paper, formulae are presented to describe the joint effects of selection and assortation on several continuous polygenic characters. The expressions extend previous work concerning these pressures as applied to a single character.

It appears that, although the results are sufficiently general to handle most of the conceivable schemes of selection and assortation with multiple characters, both of these operations would probably be carried out with respect to the selection index. A FORTRAN computer program has been written to calculate expected general gains, Δ_n, and G_n for arbitrary generation, n. This program allows complicated cases to be examined numerically by appropriate specifications, and for dimension 1, produces equivalent results to a program reported in T&L. The program is available from the author PL.

The particular numerical example involving selection for fleece characteristics illustrates the uses of the program. Moreover, it highlights efficiency advantages that can be gained by using more than a single character in the process, even when only one of the characters has economic merit.

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