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The joint effects of selection and assortative mating on a single polygenic character

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Introduction

In two previous papers (Tallis 1985, 1987), the effects of assortative mating ("assortation") and selection on additive genetic variances and covariances were examined. The arguments were sufficiently gneral to allow for the simultaneous treatment of several characters.

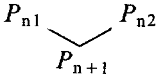
It is the purpose of this paper to extend this work by developing results which allow the joint effects of selection and assortation on genotypic and phenotypic variances to be assessed. Additional analyses also examine effects on genetic gains and on the covariances between the most important relatives. Only a single character is treated, since it is the case of prime interest. This allows the development to be simple and assists the display of ideas and results. The treatment of multiple characters is covered in a subsequent paper.

Studies such as these are important for at least two reasons: (1) it is useful to be able to assess the joint numerical effects of selection and assortation on genetic gains – there is no point in making the extra effort to mate assortatively after selection if the increase in genetic gains will be marginal; and (2) it may be required to estimate panmictic, phenotypic, and genetic variances from a population subjected to one or both of the processes. This sort of calculation was first undertaken by Fisher (1918) and the steps are given by Crow and Kimura (1970). Fisher showed that estimates of heritability of stature in man need to be corrected for positive assortation amongst the parents to reduce them to a panmictic equivalent.

Notation and basic results

A great deal of the notation and ideas of earlier papers will be used here. Thus, the processes of selection and assortation will be set in motion at generation zero, and additive genetic means and variances are examined at generation n + 1. The analysis is based on a simple pedigree structure where an individual's parents, grandparents, and so on are subjected to the processes:

Consider the pedigree



where P_{n1} and P_{n2} are the parents of individual P_{n+1} at generation n + 1. Let the attendant phenotypic and additive genetic values be p_{ni}, g_{ni} and p_{n+1}, g_{n+1}. Measurements are deviations from the generation mean and

$$V[p_{ni}] = P_n, \quad V[g_{ni}] = G_n;$$
$$V[p_{n+1}] = P_{n+1}, \quad V[g_{n+1}] = G_{n+1}.$$

At generation zero, prior to mating, selection is practiced on males and females in such a way that, if 1 refers to males and 2 to females, P_0 changes to $(1 + k_i) P_0$, i = 1, 2. This notation was first introdcued by Bulmer (1971), and it will be used here; notice that it allows for different selection pressures in the two sexes.

After selection, phenotypic assortative mating is introduced whereby the correlation between p_{01} and p_{02}, $\mathrm{cor}[p_{01}, p_{02}]$, is m_p. The parameter m_p is usually considered an invariant of the system so that, for instance, $\mathrm{cor}[p_{n1}, p_{n2}] = m_p$ also. This assumption is not mandatory as we shall see later. In any case,

$$\begin{aligned} V[p_{n1} + p_{n2}] &= 2P_n[1 + \bar{k} + \sqrt{1 + k_1}\,\sqrt{1 + k_2}\; m_p] \\ &= 2P_n + 2P_n\gamma, \text{ say} \end{aligned} \tag{1}$$

where

$\bar{k} = (k_1 + k_2)/2, \quad \gamma = [\bar{k} + \sqrt{1 + k_1}\,\sqrt{1 + k_2}\; m_p].$

Note that not only m_p but the k_i are considered invariant above. Again, this restriction will be removed.

Consider now the model

$$g_{n+1} = \tfrac{1}{2}(g_{n1} + g_{n2}) + \varepsilon, \quad E[\varepsilon] = 0, \quad V[\varepsilon] = G_0/2 \qquad (2)$$

which holds under reasonable conditions and which is independent of the fate of additive genotype further back in the pedigree (Tallis 1987). It is also assumed that

$$g_{ni} = h_n^2\, p_{ni} + \varepsilon_n \qquad (3)$$

where

$h_n^2 = G_n/P_n, \quad E[\varepsilon_n] = 0, \quad V[\varepsilon_n] = G_n(1 - h_n^2)$

and that

$$g_{n+1} = \frac{h_n^2}{2}(p_{n1} + p_{n2}) + \delta_n \qquad (4)$$

where

$E[\delta_n] = 0 \quad \text{and} \quad V[\delta_n] = \tfrac{1}{2}(G_0 + G_n - h_n^4 P_n).$

If p_{n1} and p_{n2} are subjected to selection followed by assortation

$$V[g_{n+1}] = G_{n+1} = \frac{h_n^4}{4}[2P_n + 2P_n\gamma] + V[\delta_n]$$

$$= \frac{G_n}{2} + \frac{G_0}{2} + G_n h_n^2 \frac{\gamma}{2}. \qquad (5)$$

Subtracting G_0 from both sides and putting $G_n - G_0 = D_n$, the "disequilibrium variance",

$$D_{n+1} = \frac{D_n}{2} + G_n h_n^2 \frac{\gamma}{2} = \gamma \sum_{i=0}^{n} 2^{-(n+1-i)} G_i h_i^2. \qquad (6)$$

It is not necessary that k_1, k_2 and m_p remain constant from generation to generation. In fact, if P_n changes to $(1 + k_{ni})P_n$, $i = 1, 2$, and $\mathrm{cor}[p_{n1}, p_{n2}] = m_{np}$, let

$\gamma_n = (\bar{k}_n + \sqrt{1 + k_{n1}}\,\sqrt{1 + k_{n2}}\; m_{np}).$

Then

$$D_{n+1} = \frac{D_n}{2} + G_n h_n^2 \frac{\gamma_n}{2} = \sum_{i=0}^{n} 2^{-(n+1-i)} G_i h_i^2 \gamma_i. \qquad (7)$$

This result can be argued in the same manner as Bulmer (1971). At G_1 the disequilibrium variance as a result of selection and assortation at G_0, D_1, is $\frac{1}{2} G_0 h_0^2 \gamma_0$ which contributes $2^{-(n+1)} G_0 h_0^2 \gamma_0$ to D_{n+1}. Similarly, at G_{i+1} the increase in disequilibrium variance due to selection and assortation at G_i is $G_i h_i^2 \gamma_i/2$ which contributes $2^{-(n+1-i)} G_i h_i^2 \gamma_i$ to D_{n+1}. Summing from $i = 0$ to $i = n$ gives the required formula.

Now, provided γ_t tends to a limit, say $\bar{\gamma}$, the equilibrium equation is

$$\hat{D} = \bar{\gamma}\hat{G}\hat{h}^2, \quad \hat{h}^2 = \hat{G}/\hat{P}, \quad \hat{G} = G_0 + \hat{D}, \quad \hat{P} = P_0 + \hat{D} \qquad (8)$$

with solution

$$\hat{D} = P_0\{2\bar{\gamma}h_0^2 - 1 + [1 - 4\bar{\gamma}h_0^2(1 - h_0^2)]^{1/2}\}/2(1 - \bar{\gamma}) \qquad (9)$$

(see Bulmer (1971) Eqn. 19).

Equilibrium covariance between relatives

The effect of both selection and assortation on the covariance between full-sibs, half-sibs and parent-offspring will now be derived with the aid of "transfer systems", which were introduced and extensively used in Tallis (1985). These systems will not be discussed here in detail, but their basic property is described below.

Let $\{X_1, X_2, \ldots, X_n\}$ be a set of random variables satisfying the conditions of a transfer system, T.S., then

$$C[X_1, X_n] = C[X_1, X_2]\,V[X_2]^{-1}\,C[X_2, X_3]\,V[X_3]^{-1} \ldots C[X_{n-1}, X_n]. \qquad (10)$$

To analyse the following pedigrees, one requires two T.S.'s: (1) the mating T.S. (M.T.S.), (2) the pedigree T.S. (P.T.S.).

For full-sibs and parent-offspring the M.T.S. is that governing phenotypic assortative mating, namely $S_p = \{g_{n1}, p_{n1}, p_{n2}, g_{n2}\}$ at generation n. Half-sibs require, in addition to S_p, a special M.T.S. which will be given later. The T.S.'s used here are those used in the 1985 paper, and the assumption is that these systems are pertinent, even in the presence of selection and assortation.

Define the following quantities

$\hat{G} = G_0 + \hat{D}, \quad \hat{P} = P_0 + \hat{D}, \quad \hat{h}^2 = \hat{G}/\hat{P},$

$\hat{V}[\hat{g}_{0i}] = \hat{G}_i = \hat{G} + \hat{G}\hat{h}^2 k_i, \quad \hat{V}[\hat{p}_{0i}] = \hat{P}_i = (1 + k_i)\hat{P},$

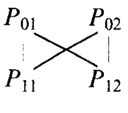
$\hat{C}[\hat{g}_{0i}, \hat{p}_{0i}] = \hat{h}^2\hat{P}_i, \quad i = 1, 2$

$\hat{C}_p = \hat{P}\sqrt{1 + k_1}\,\sqrt{1 + k_2}\; m_p,$

$\hat{\mathrm{cov}}[\hat{g}_{01}, \hat{g}_{02}] = \hat{C}_g = \hat{h}^4\hat{C}_p.$

The formula for $\hat{C}_g$ is found from S_p by using (10) with the above results and going to equilibrium values, while $\hat{G}_i$ and $\hat{C}[\hat{g}_{0i}, \hat{p}_{0i}]$ follow from the assumed model $\hat{g} = \hat{h}^2\hat{p} + \varepsilon$, $\hat{p}$ and ε independent and $V[\varepsilon] = \hat{G}(1 - \hat{h}^2)$.

Full-sibs

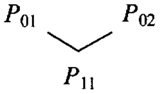


M.T.S. $S_p = \{\hat{g}_{01}, \hat{p}_{01}, \hat{p}_{02}, \hat{g}_{02}\}$

P.T.S $\{\hat{p}_{11}, \hat{g}_{11}, \hat{g}_{12}, \hat{p}_{12}\}$

$$\begin{aligned}\hat{C}[S,S] &= C[\hat{p}_{11},\hat{p}_{12}] = C[\hat{p}_{11},\hat{g}_{11}]\,V[\hat{g}_{11}]^{-1}\\ &\quad\cdot C[\hat{g}_{11},\hat{g}_{12}]\,V[\hat{g}_{12}]^{-1}\,C[\hat{g}_{12},\hat{p}_{12}]\\ &= \hat{G}\,\hat{G}^{-1}\,C[\tfrac{1}{2}(\hat{g}_{01}+\hat{g}_{02}),\ \tfrac{1}{2}(\hat{g}_{01}+\hat{g}_{02})]\,\hat{G}^{-1}\,\hat{G}\\ &= \tfrac{1}{4}[\hat{G}_1+\hat{G}_2+2\,\hat{C}_g]\\ &= \frac{\hat{G}}{2}[1+\bar{k}\,\hat{h}^2+\hat{G}^{-1}\,\hat{C}_g].\end{aligned}$$

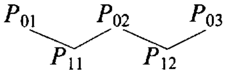
Parent-offspring



M.T.S. $S_p = \{\hat{g}_{01}, \hat{p}_{01}, \hat{p}_{02}, \hat{g}_{02}\}$
P.T.S. $\{\hat{p}_{01}, \hat{g}_{11}, \hat{p}_{11}\}$

$$\begin{aligned}\hat{C}[P,0] = C[\hat{p}_{01},\hat{p}_{11}] &= C[\hat{p}_{01},\hat{g}_{11}]\,V[\hat{g}_{11}]^{-1}\,C[\hat{g}_{11},\hat{p}_{11}]\\ &= C[\hat{p}_{01},\tfrac{1}{2}(\hat{g}_{01}+\hat{g}_{02})]\\ &= \frac{\hat{P}_1\,\hat{h}^2}{2}+\tfrac{1}{2}\,C[\hat{p}_{01},\hat{g}_{02}]\\ &= \frac{\hat{P}_1\,\hat{h}^2}{2}+\tfrac{1}{2}\,\hat{C}_p\,\hat{h}^2 \quad (\text{from } S_p)\\ &= \frac{\hat{h}^2}{2}(\hat{P}_1+\hat{C}_p).\end{aligned}$$

Half-sibs (P_{01}, P_{03} female, P_{02} male)



M.T.S. $\{\hat{g}_{01}, \hat{p}_{01}, \hat{p}_{02}, \hat{p}_{03}, \hat{g}_{03}\}$
$\{\hat{g}_{01}, \hat{p}_{01}, \hat{p}_{02}, \hat{g}_{02}\}$
$\{\hat{g}_{02}, \hat{p}_{02}, \hat{p}_{03}, \hat{g}_{03}\}$
P.T.S. $\{\hat{p}_{11}, \hat{g}_{11}, \hat{g}_{12}, \hat{p}_{12}\}$

$$\begin{aligned}C[\tfrac{1}{2}S,\tfrac{1}{2}S] &= C[\hat{p}_{11},\hat{p}_{12}] = \hat{G}\,\hat{G}^{-1}\,C[\hat{g}_{11},\hat{g}_{12}]\,\hat{G}^{-1}\,\hat{G}\\ &= C[\tfrac{1}{2}(\hat{g}_{01}+\hat{g}_{02}),\ \tfrac{1}{2}(\hat{g}_{02}+\hat{g}_{03})]\\ &= \tfrac{1}{4}(C[\hat{g}_{01},\hat{g}_{02}]+C[\hat{g}_{01},\hat{g}_{03}]+V[\hat{g}_{02}]\\ &\quad + C[\hat{g}_{02},\hat{g}_{03}])\\ &= \tfrac{1}{4}(\hat{G}_1+2\,\hat{C}_g+\hat{h}^4\,\hat{P}_2\,m_p^2).\end{aligned}$$

With minor adjustments these formulae conform with those of Tallis (1985), Table 1, when selection is absent. Other pedigrees can be handled similarly, but complications arise from the application of selection in each generation. Ensuing formulae are objectionable and the matter will not be pursued further since the most useful relationships have been considered. Of course, results for selection only are obtained by putting $m_p = 0$.

Consider, finally, the reverse problem. The parameters $\hat{P}$ and $\hat{C}[P,0]$, say, are given and it is required to calculate G_0 and P_0. Note that $\hat{P}$ and $\hat{C}[P,0]$ are both directly estimable in the equilibrium population.

Let $\theta = \sqrt{1+k_1}\,\sqrt{1+k_2}\,m_p$, $\hat{C} = \hat{C}[P,0]$, then both G_0 and P_0 can be found from the following equations:

$$\hat{G} = 2\,\hat{C}/(1+k+\theta) \tag{11}$$

$$\hat{D} = \hat{G}\,\hat{h}^2\,\bar{\gamma},\ \hat{h}^2 = \hat{G}/\hat{P};\quad \hat{G} = G_0+\hat{D},\ \hat{P} = P_0+\hat{D}.$$

Numerical results and discussion

Equation (4) allows the expected genetic gain under truncation selection, Δ_n, to be calculated as a function of m_p and the proportions saved of each parent population, α_1 and α_2.

Thus, putting $\phi(x) = \dfrac{e^{-x^2}}{\sqrt{2\pi}}$ and $\Phi(x) = \int_{-\infty}^{x} \phi(t)\,dt$ leads to standardised truncation points, a_i, where $1-\alpha_i = \Phi(a_i)$, $i = 1, 2$.

Hence

$$\Delta_n = \sqrt{P_{n-1}}\,h_{n-1}^2\,\bar{\tau} \tag{12}$$

where

$$\bar{\tau} = (\tau(a_1)+\tau(a_2))/2,\quad \tau(a_i) = \frac{\phi(a_i)}{1-\Phi(a_i)}.$$

Since Δ_n is a function of h_0^2, α_1, α_2 and m_p, Δ_n is rewritten as $\Delta_n(h_0^2,\alpha_1,\alpha_2,m_p)$. The efficiency is then measured as

$$\begin{aligned}E_n(h_0^2,\alpha_1,\alpha_2,m_p) = \Delta_n(h_0^2,\alpha_1,\alpha_2,m_p)/\\ \Delta_n(h_0^2,\alpha_1,\alpha_2,0).\end{aligned} \tag{13}$$

Values of E for large n, E_∞, are given in Table 1.

Table 1 shows what advantages can be expected from positive phenotypic assortation. The percent efficiency rises with the heritability. It also decreases as the proportion of individuals saved decreases.

Under low intensities of selection, the genetic gain using close assortation can be increased from 15% to 50%. However, for selection proportions of 0.2 or less, the increase in efficiency is at most 5%. These observations suggest that in sheep and cattle breeding, assortative mating may be more trouble than it is worth.

It is of some interest to explore the effect on genetic gain of a number, n_1, of generations of assortative mating without selection, followed by combined assortation and selection for n_2 generations, $n_1 + n_2 = n$.

To this end, an interactive computer program has been written in FORTRAN and source listings are available from P. Leppard at the above address. Required input values are n, P_0, G_0, α_1, α_2 and n_1. Table 2 gives the results for 5, 1, 0.5, 0.2, 0.2, and 1.

Table 1. E_{∞} (h_0^2, α_1, α_2, m_p) − 100

α_1	α_2	m_p	h_0^2					
			0.05	0.2	0.4	0.6	0.8	1.0
0.9	0.9	−1.0	−3.13	−9.34	−14.12	−17.08	−18.95	−19.75
		−0.5	−1.61	−5.09	−7.98	−9.84	−11.01	−11.49
		0.5	1.72	6.28	11.09	14.59	16.78	17.56
		1.0	3.57	14.39	28.44	40.11	47.29	49.55
0.9	0.5	−1.0	−2.23	−6.57	−9.89	−11.95	−13.28	−13.87
		−0.5	−1.14	−3.49	−5.39	−6.59	−7.37	−7.71
		0.5	1.19	4.01	6.63	8.42	9.57	10.03
		1.0	2.44	8.69	15.12	19.76	22.73	23.83
0.9	0.2	−1.0	−1.73	−5.11	−7.69	−9.30	−10.34	−10.81
		−0.5	−0.88	−2.67	−4.11	−5.02	−5.61	−5.87
		0.5	0.91	2.97	4.79	6.01	6.80	7.12
		1.0	1.85	6.29	10.49	13.40	15.28	16.02
0.9	0.05	−1.0	−1.38	−4.08	−6.15	−7.45	−8.30	−8.68
		−0.5	−0.70	−2.12	−3.24	−3.96	−4.43	−4.63
		0.5	0.72	2.29	3.65	4.55	5.14	5.38
		1.0	1.45	4.80	7.82	9.87	11.20	11.74
0.5	0.5	−1.0	−1.57	−4.57	−6.82	−8.21	−9.12	−9.54
		−0.5	−0.80	−2.38	−3.61	−4.39	−4.90	−5.13
		0.5	0.83	2.61	4.13	5.13	5.78	6.06
		1.0	1.68	5.50	8.92	11.24	12.75	13.38
0.5	0.2	−1.0	−1.22	−3.53	−5.25	−6.32	−7.02	−7.35
		−0.5	−0.62	−1.82	−2.74	−3.33	−3.71	−3.88
		0.5	0.63	1.95	3.03	3.73	4.19	4.40
		1.0	1.28	4.05	6.41	7.96	8.99	9.43
0.5	0.05	−1.0	−0.97	−2.80	−4.17	−5.02	−5.58	−5.85
		−0.5	−0.49	−1.44	−2.16	−2.62	−2.92	−3.06
		0.5	0.50	1.52	2.33	2.86	3.21	3.36
		1.0	1.01	3.12	4.87	6.01	6.76	7.09
0.2	0.2	−1.0	−0.94	−2.71	−4.02	−4.83	−5.37	−5.62
		−0.5	−0.48	−1.39	−2.08	−2.51	−2.80	−2.93
		0.5	0.48	1.46	2.24	2.74	3.07	3.22
		1.0	0.98	3.01	4.66	5.74	6.45	6.77
0.2	0.05	−1.0	−0.75	−2.15	−3.18	−3.82	−4.25	−4.45
		−0.5	−0.38	−1.09	−1.63	−1.97	−2.20	−2.30
		0.5	0.38	1.14	1.73	2.11	2.36	2.47
		1.0	0.77	2.33	3.57	4.37	4.90	5.14
0.5	0.05	−1.0	−0.59	−1.70	−2.51	−3.02	−3.35	−3.51
		−0.5	−0.30	−0.86	−1.28	−1.55	−1.72	−1.80
		0.5	0.30	0.89	1.34	1.63	1.82	1.91
		1.0	0.61	1.81	2.75	3.34	3.74	3.93

Table 2. Display produced by computer program with input (5, 1, 0.5, 0.2, 0.2, 1)

Generation	$M_p = 0.00$	$M_p = 1.00, n_l = 0$		$M_p = 1.00, n_l = 1$	
	Delta (g)	Delta (g)	E (g)	Delta (g)	E (g)
1	0.6999	0.6999	100.00	0.0000	0.00
2	0.5929	0.6238	105.21	0.8248	139.12
3	0.5683	0.6005	105.66	0.6624	116.56
4	0.5625	0.5933	105.47	0.6123	108.84
5	0.5612	0.5911	105.34	0.5969	106.38
Total gain	2.9848	3.1086	104.15	2.6965	90.34

As expected, the generation by generation gains are generally greater following a period of straight assortative mating. However, the total progress is greater for combined assortation and selection starting at generation zero. This is because in these cases the lack of progress in generations of no selection is never retrieved in spite of increased gains in subsequent generations.

It should be noted that column 2 of Table 2 corresponds to Table 1 of Bulmer (1971). Table 2 of Smith and Hammond (1987) can also be obtained using this program with specifications $n = 2$, $m_p = 1$ and the appropriate choices of α_1, α_2 and h^2.

References

Bulmer MG (1971) The effect of selection on genetic variability. Am Nat 105:201–211

Crow JF, Kimura M (1970) An introduction to population genetic theory. Burgess, Minneapolis, Minn

Fisher RA (1918) The correlation between relatives on the supposition of Mendelian inheritance. Trans R Soc Edinburgh 52:399–433

Smith SP, Hammond K (1987) Assortative mating and artificial selection: a second appraisal. Genet Sel Evol 19:181–196

Tallis GM (1985) Transfer systems and covariance under assortative mating. Theor Appl Genet 70:497–504

Tallis GM (1987) Ancestral covariance and the Bulmer effect. Theor Appl Genet 73:815–820