

## A note on non-random mating in progeny tests

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### 1. INTRODUCTION

It is well known that the regression of progeny on mid-parent value in a random-mating population measures the additive genetic fraction of the phenotypic variance of that population, for any quantitative character, and this relationship has often been used to estimate the heritability of such characters. In practice, such progeny tests are often limited in size for technical reasons, and lead to estimates of the regression coefficient with such large standard errors as to be virtually useless.

Statistically more accurate estimates can be obtained with the same sample size by mating parents assortatively (like with like), or in any other way which increases the mid-parent variance—e.g. by selecting only plus and minus extremes as parents, which may be combined with assortative mating. The variance of the regression coefficient will obviously be reduced in the same proportion as the variance of mid-parent phenotype is increased.

This method was proposed, with some reservations, by Reeve (1953), but has been criticized by Wright (1952) on the grounds that assortative mating must introduce correlations between the non-additive genetic effects of parents and offspring, and so will lead to an unpredictable bias in the regression estimate. Reeve (1955), in a brief contribution which is untitled and buried deeply in the discussion pages of the reference in question, gave a mathematical argument to show that the bias from non-random mating will often be negligible, but the problem needs rather more detailed examination, which I shall attempt to give here. The effects of assortative mating on the correlation between sibs will also be considered.

### 2. THE REGRESSION OF PROGENY ON MID-PARENT

#### (i) *Effects of assortative mating*

Consider a population in equilibrium under random mating, in which a character, say body size, is normally distributed with phenotypic standard deviation  $\sigma$ . We want to know in what way the regression of progeny on mid-parent will be affected, if we draw a random sample of each sex from the population and then mate them assortatively for body size, so as to introduce a correlation  $\mu$  between mates.

It is mathematically more convenient to suppose that an infinitely large sample of each sex is drawn at random, and assortative mating introduced so that body size of the two sexes follows a bivariate normal distribution with correlation coefficient  $\mu$ . The sample of pairs chosen for our progeny test may then be supposed to have been picked at random from this correlated population. The usual procedure of picking samples of each sex at random and then mating them assortatively may not give precisely a random sample from a bivariate normal distribution, if the correlation is high, but any deviation in practice from our model is not likely to be appreciable.

We consider now a single pair of alleles A and B, with frequencies  $p$  and  $q = 1 - p$ . The complete population consists of the three sub-populations of genetic constitutions AA, AB and BB. Let the means of these be  $a, b$  and  $c$ , respectively; and let us choose the origin so that  $p^2a + 2pqb + q^2c = 0$ . If there is any sex difference in size or variance, this may be eliminated by a suitable transformation.

It will be assumed that all gene substitution effects such as  $a, b$  or  $c$  are small compared with the phenotypic standard deviation, so that the standard deviation of each sub-population can be taken as approximately  $\sigma$ .

Then the probability that a particular male parent in our sample is of genotype AA and size  $x$  is

$$P(x, a) = \frac{p^2}{\sigma(2\pi)^{1/2}} \exp \left[ -\frac{(x-a)^2}{2\sigma^2} \right] dx, \tag{1}$$

and the probability that a particular female parent is of genotype AB and size  $y$  is

$$P(y, b) = \frac{2pq}{\sigma(2\pi)^{1/2}} \exp \left[ -\frac{(y-b)^2}{2\sigma^2} \right] dy, \tag{2}$$

but the probability that a pair of mates have these sizes and genetic constitutions is, in view of the correlation between mates,

$$\begin{aligned} P(x, a; y, b) &= P(x, a) \cdot P(y, b) \frac{1}{(1-\mu^2)^{1/2}} \exp \left[ -\frac{\mu^2 x^2 - 2\mu xy + \mu^2 y^2}{2\sigma^2(1-\mu^2)} \right] \\ &= \frac{2p^3 q}{2\pi\sigma^2(1-\mu^2)^{1/2}} \exp \left[ -\frac{(1-\mu^2)\{(x-a)^2 + (y-b)^2\} + \mu^2(x^2 + y^2) - 2\mu xy}{2\sigma^2(1-\mu^2)} \right] dx \cdot dy. \end{aligned} \tag{3}$$

By integrating (3) over the ranges of  $x$  and  $y$ , we obtain the total frequency of matings between AA males and AB females as  $p^2 \cdot 2pq \cdot \exp[\mu ab/\sigma^2]$ . This treatment and result are due to Fisher (1918), and we shall use these overall frequencies later in considering the effects of assortative mating on the correlation between sibs (see also Kempthorne, 1957, pp. 492-4).

To find the regression of progeny on mid-parent, we need to determine the progeny mean for a given mid-parent value  $X = \frac{1}{2}(x+y)$ . Substituting  $y = (2X - x)$

in (3) and rearranging terms, we obtain

$$P(x, a; 2X - x, b) = \frac{2p^3 q}{\pi\sigma^2(1 - \mu^2)^{1/2}} \exp \left[ \frac{\mu ab}{\sigma^2} - \frac{\{x - X - \frac{1}{2}(1 - \mu)(a - b)\}^2}{\sigma^2(1 - \mu)} - \frac{\{X - \frac{1}{2}(1 + \mu)(a + b)\}^2}{\sigma^2(1 + \mu)} \right] dx \cdot dX \quad (4)$$

for the probability that a pair of mates of sizes  $x$  and  $(2X - x)$  have the genetic constitutions AA and AB, respectively. Integrating out  $x$ , we obtain the relative frequency of matings with male and female parents AA and AB and mid-parent size  $X$  as

$$P(X; a, b) = P(X; b, a) = \frac{2p^3 q}{\sigma\{\pi(1 + \mu)\}^{1/2}} \exp \left[ \frac{\mu ab}{\sigma^2} - \frac{\{2X - (1 + \mu)(a + b)\}^2}{4\sigma^2(1 + \mu)} \right] \cdot dX. \quad (5)$$

Now write  $X = k\sigma$ , giving, after some simplification,

$$P(k\sigma; a, b) = \frac{2p^3 q e^{-k^2/1 + \mu}}{\sigma\{\pi(1 + \mu)\}^{1/2}} \exp \left[ \frac{k(a + b)}{\sigma} - \frac{(a + b)^2 + \mu(a - b)^2}{4\sigma^2} \right] \sigma \cdot dk. \quad (6)$$

Expanding the exponential in terms of  $1/\sigma$ , and omitting constant terms which do not change when  $c$  is substituted for  $a$  or  $b$ , the frequency is proportional to

$$2p^3 q \left[ 1 + \frac{k(a + b)}{\sigma} + \frac{(2k^2 - 1)(a + b)^2 - \mu(a - b)^2}{4\sigma^2} + \text{terms in } 1/\sigma^3 \text{ etc.} \right]. \quad (7)$$

Since individual substitution effects are assumed to be small compared with  $\sigma$ , we can ignore terms in  $1/\sigma^2$  and higher powers of  $1/\sigma$ , and (6) reduces to

$$P(k\sigma; a, b) = \text{Constant} \times p^2 \cdot 2pq \left[ 1 + \frac{k(a + b)}{\sigma} \right] \cdot dk. \quad (8)$$

Substituting  $b = a$ ,  $b = c$ , etc. in (8) gives the relative frequencies of matings of each type shown in Table 1.

Table 1. *Mating frequencies with mid-parent  $k/\sigma$ , after assortative mating*

Mating	Frequency ( $f$ )	Progeny mean ( $\bar{O}$ )
AA × AA	$p^4 \left\{ 1 + 2\frac{k}{\sigma} a \right\}$	$a$
AA × AB	$4p^3 q \left\{ 1 + \frac{k}{\sigma} (a + b) \right\}$	$\frac{1}{2}(a + b)$
AA × BB	$2p^3 q^2 \left\{ 1 + \frac{k}{\sigma} (a + c) \right\}$	$b$
AB × AB	$4p^2 q^2 \left\{ 1 + 2\frac{k}{\sigma} b \right\}$	$\frac{1}{2}(a + 2b + c)$
AB × BB	$4pq^3 \left\{ 1 + \frac{k}{\sigma} (b + c) \right\}$	$\frac{1}{2}(b + c)$
BB × BB	$q^4 \left\{ 1 + 2\frac{k}{\sigma} c \right\}$	$c$

Since the terms containing  $\mu$  in (7) are at most of order  $1/\sigma^2$ , they are eliminated from (8) and from Table 1. It follows immediately that, assuming we can ignore terms in  $1/\sigma^2$ , a phenotypic correlation between mates will have no appreciable effect on the progeny mean for a given mid-parent size, and so will not bias the regression of progeny on mid-parent.

We notice, in fact, that the frequencies ( $f$ ) in Table 1 add to unity, since the sum of terms in  $k/\sigma$  has a factor  $p^2a + 2pqb + q^2c = 0$ . Multiplying the frequencies by the progeny means ( $\bar{O}$ ), also given in the table, and adding over matings, the progeny mean for all matings with mid-parent phenotype  $k\sigma$  is seen to be

$$\sum f\bar{O} = 2pq\{p(a-b) + q(b-c)\}^2 k/\sigma, \tag{9}$$

which is  $k/\sigma$  times the additive genetic variance due to the gene pair A,B. Since  $\sum f\bar{O} = 0$  when  $X = k\sigma = 0$ , the regression coefficient of progeny on mid-parent is

$$\sum f\bar{O}/X = 2pq\{p(a-b) + q(b-c)\}^2/\sigma^2, \tag{10}$$

which is the usual formula for random mating.

Evidently non-additive intra-locus gene effects will not bias the regression, under the conditions assumed. But, since  $\mu$  only appears in (7) in terms of order  $1/\sigma^2$  and less, it is clear that a correlation between mates will not bias the regression even when interactions between loci occur, since it can only introduce a disturbance of the second order.

(ii) *Effects of selection of parents*

One might guess that selection of parents so as to increase their variance over that of the general population would also leave the regression coefficient virtually unchanged given the same conditions, and this may be shown by the following argument.

Suppose we select only parents which differ from the population mean (taken as zero) by at least  $\pm t\sigma$ , and mate selected males and females together at random except that males from the plus group are mated to females from the plus group, and minus to minus. This is what generally happens when a generation of two-way selection is carried out.

We require first the mid-parent mean for each group, which will be the same as the mean for each sex, since both sexes are assumed to have the same variance.

These means are

$$\bar{x} = \pm \frac{1}{\sigma(2\pi)^{1/2}} \int_{t\sigma}^{\infty} x e^{-x^2/2\sigma^2} dx \Big/ \frac{1}{\sigma(2\pi)^{1/2}} \int_{t\sigma}^{\infty} e^{-x^2/2\sigma^2} dx = \frac{\sigma}{(2\pi)^{1/2}} e^{-t^2} \{1 - F(t)\}, \tag{11}$$

where  $F(t)$  is the distribution function  $\frac{1}{(2\pi)^{1/2}} \int_{-\infty}^t e^{-y^2} dy$ .

Now the probability that a parent in the plus group is drawn from the AA sub-population with mean  $a$  and variance  $\sigma^2$  is

$$P(a) = \frac{Lp^2}{\sigma(2\pi)^{1/2}} \int_{t\sigma-a}^{\infty} e^{-x^2/2\sigma^2} dx = Lp^2 \left\{ 1 - F\left(t - \frac{a}{\sigma}\right) \right\} \tag{12}$$

where  $L$  is a constant to be determined so that the similar expressions  $P(a)$ ,  $P(b)$  and  $P(c)$  add to unity. But since  $a/\sigma$  is small, we have

$$\begin{aligned} 1 - F\left(t - \frac{a}{\sigma}\right) &= 1 - F(t) + \frac{1}{(2\pi)^{1/2}} \int_{t-(a/\sigma)}^t e^{-t^2x} dx \\ &\sim 1 - F(t) + \frac{1}{(2\pi)^{1/2}} \frac{a}{2\sigma} \{e^{-t^2} + e^{-t[t-(a/\sigma)]}\}. \end{aligned}$$

On expanding the exponential terms involving  $a$ , we have, with sufficient accuracy,

$$1 - F\left(t - \frac{a}{\sigma}\right) = 1 - F(t) + \frac{e^{-t^2}}{(2\pi)^{1/2}} \left\{ \frac{a}{\sigma} + \frac{ta^2}{2\sigma^2} + \frac{(t^2-1)a^3}{4\sigma^3} + \dots \right\} \tag{13}$$

Substituting in (12) and ignoring terms in  $1/\sigma^2$  etc., we obtain

$$P(a) = Lp^2 \left\{ 1 - F(t) + \frac{a}{\sigma(2\pi)^{1/2}} e^{-t^2} \right\}. \tag{14}$$

$P(b)$  and  $P(c)$  are obtained from (14) by substituting  $b$  and  $c$  for  $a$ , and  $2pq$  and  $q^2$  for  $p^2$ , respectively; and since these three probabilities add to unity and  $p^2a + 2pqb + q^2c = 0$ , we find

$$\begin{aligned} L &= 1/\{1 - F(t)\} \\ \text{so that} \quad & \left. \begin{aligned} P(a) &= p^2 \left\{ 1 + C \frac{a}{\sigma} \right\} \\ P(b) &= 2pq \left\{ 1 + C \frac{b}{\sigma} \right\} \\ P(c) &= q^2 \left\{ 1 + C \frac{c}{\sigma} \right\} \end{aligned} \right\} \tag{15} \end{aligned}$$

where  $C = e^{-t^2}/(2\pi)^{1/2}\{1 - F(t)\}$ .

It is now easy to obtain the mean progeny value for matings within the plus group, since the frequencies are  $\{P(a)\}^2$  for AA  $\times$  AA matings,  $2P(a).P(b)$  for AA  $\times$  AB matings, etc., and the progeny mean for each mating type is given in Table 1. Ignoring terms in  $1/\sigma^2$ ,

$$\{P(a)\}^2 = p^4 \{1 + 2Ca/\sigma\}, \quad 2P(a).P(b) = 4p^3q \{1 + C(a+b)/\sigma\},$$

etc., so that the frequencies become identical with those given in Table 1, except that  $C$  is substituted for  $k$ . We thus have immediately from (9),

$$\sum f\bar{O} = 2pq \{p(a-b) + q(b-c)\}^2 C/\sigma \tag{16}$$

for the plus group, while minus this value is the progeny mean for the minus group of matings.

The regression of progeny on mid-parent is, therefore, (16)÷(11), i.e.

$$\Sigma f\bar{O}/\bar{x} = 2pq\{p(a-b) + q(b-c)\}^2/\sigma^2, \quad (17)$$

which is the same as (10). It may be seen from (13) that deviations from this value due to the selection of parents are of the order of  $1/\sigma^2$ .

Clearly, given our assumption that individual gene substitution effects are small compared with the phenotypic standard deviation, neither selection of parents nor assortative mating, nor indeed a combination of the two, will introduce an appreciable bias into the regression coefficient of progeny on mid-parent, regardless of the presence of interactions within and between loci. The effect of these methods of increasing the mid-parental variance will be almost confined to reducing the sampling variance of the regression coefficient.

Equations (15) are of some interest, as they give the relative frequencies of the three phases of any pair of alleles A,B among individuals selected so as to be at least  $k\sigma$  units above the population mean. We notice that

$$\begin{aligned} P(a).P(c) - \frac{1}{4}P^2(b) &= p^2 q^2 (a - 2b + c)^2 C^2 / \sigma^2 \\ &= C^2 \sigma_D^2 / \sigma^2, \end{aligned}$$

where  $\sigma_D^2$  is the genetic variance due to dominance at the (A,B) locus. This shows that the extent to which the three phases of a gene pair are out of equilibrium in such a selected population is a function of the intensity of selection and the amount of dominance.

Equations (9) and (16) differ only in the substitution of  $C$  for  $k$  in the latter, and it is of interest to compare these two coefficients more directly. If  $X$  is a given mid-parent size in the correlated population, and  $\bar{x}$  is the mean of parents deviating from the population mean by at least  $+\sigma$  units in the case of selected parents, then we have

$$\begin{aligned} k &= X/\sigma, \\ C &= \bar{x}/\sigma. \end{aligned}$$

This brings out clearly the equivalence of the two coefficients.

### 3. THE CORRELATION BETWEEN SIBS AFTER ASSORTATIVE MATING

When the genetic variance is entirely additive, a correlation  $\mu$  between mates has no effect on the regression coefficient of progeny on mid-parent, since both the numerator and denominator of this coefficient are multiplied by the same factor  $(1 + \mu)$ . The covariance between sibs and the progeny variance are, however, multiplied by different factors, so that the correlation between sibs is changed in the ratio  $(1 + \mu h^2)/(1 + \frac{1}{2}\mu h^4)$ , as shown by Reeve (1953). We might expect, therefore, that the bias from non-additive effects would be greater for the sib-correlation than for the regression, after assortative mating. An examination of the two-allele case will show that this is so.

Terminology here presents a problem, since there has been a confusing variety in the symbols used by different authors for the same genetic parameters (compare, for example, the symbols used by Kempthorne, 1957, and Falconer, 1960). I shall therefore first summarize the definitions and basic formulae used in the present analysis.

As before, the three phases at the (A,B) locus have phenotypic values  $a, b$  and  $c$ , the gene frequencies being  $p$  and  $q$ , and the total phenotypic variance  $\sigma^2$ . Let  $\sigma_G^2, \sigma_A^2$ , and  $\sigma_D^2$  be the total genetic variance and the contributions to it of additive and dominance effects, for this particular locus, in the random-mating population. Then

$$\begin{aligned} \sigma_G^2 &= p^2 a^2 + 2pqb^2 + q^2 c^2, \\ \sigma_A^2 &= 2pq\{p(a-b) + q(b-c)\}^2 = 2pq(b^2 - ac), \\ \sigma_D^2 &= p^2 q^2(a - 2b + c)^2 = (pa + qc)^2. \end{aligned}$$

Let  $A = p(a - b) + q(b - c)$ , whence  $\sigma_A^2 = 2pqA^2$ ,

$D = -pq(a - 2b + c)$ , whence  $\sigma_D^2 = D^2$ .

Then  $A$  is the average substitution effect and  $D$  the mean dominance deviation. Both these terms occur in the formula for the correlation between sibs after assortative mating.

As we saw earlier, the introduction of a correlation  $\mu$  between mates has the effect of multiplying the frequency of matings between AA and AB by the factor  $\exp(\mu ab/\sigma^2)$ , with similar factors for other matings. Assuming that the individual substitution effects are small compared with the phenotypic standard deviation, we can write this expression as  $\{1 + (\mu ab/\sigma^2)\}$ , which leads to the correlation table for sibs, following one generation of assortative mating, shown in Table 2. This case should not be confused with the one discussed by Fisher (1918), where the population is in equilibrium under a small degree of continued assortative mating.

Table 2 also gives the total frequency of occurrence of each of the three genotypes among the progeny, so that we can calculate from it the mean phenotype of progeny ( $\bar{O}$ ), the covariance between sibs  $\text{cov}(O, O)$ , and the genetic variance in the progeny generation due to the gene pair (A,B), which will be called  $\sigma_{G_1}^2$ . All three indices lead to rather heavy algebraic expressions, which can be simplified into the following formulae:

$$\bar{O} = \sum fO = -\frac{1}{2} \frac{\mu}{\sigma^2} D\sigma_A^2,$$

$$\text{cov}(O, O) = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2 + \frac{\mu}{\sigma^2} K_1 - \frac{1}{4} \frac{\mu^2}{\sigma^4} \sigma_D^2 \sigma_A^4,$$

$$\sigma_{G_1}^2 = \sigma_A^2 + \sigma_D^2 + \frac{\mu}{\sigma^2} K_2 - \frac{1}{4} \frac{\mu^2}{\sigma^4} \sigma_D^2 \sigma_A^4,$$

where

$$K_1 = [\sigma_A^2 + \frac{1}{2}\sigma_D^2 + \frac{1}{2}(p - q)AD]^2 - \frac{1}{2}\sigma_A^4$$

and

$$K_2 = \frac{1}{2}\sigma_A^2 \left[ 2pq \left\{ A + \frac{p - q}{pq} D \right\}^2 - \frac{(p - q)^2}{pq} \sigma_D^2 \right].$$

Table 2. *Correlation table for sib-pairs after assortative mating*

Sib-pair	Frequency ( <i>f</i> ) of occurrence together
AA, AA ( <i>a, a</i> )	$p^2(p + \frac{1}{2}q)^2 + \frac{\mu}{\sigma^2}[p^2(pa + \frac{1}{2}qb)^2]$
AA, AB ( <i>a, b</i> )	$2p^2q(p + \frac{1}{2}q) + \frac{\mu}{\sigma^2}[2p^2qb(pa + \frac{1}{2}qb)]$
AA, BB ( <i>a, c</i> )	$\frac{1}{2}p^2q^2 + \frac{\mu}{\sigma^2}[\frac{1}{2}p^2q^2b^2]$
AB, AB ( <i>b, b</i> )	$pq(1 + pq) + \frac{\mu}{\sigma^2}[2pq(pa + \frac{1}{2}qb)(\frac{1}{2}pb + qc) + \frac{1}{2}p^2q^2b^2]$
AB, BB ( <i>b, c</i> )	$2pq^2(\frac{1}{2}p + q) + \frac{\mu}{\sigma^2}[2pq^2b(\frac{1}{2}pb + qc)]$
BB, BB ( <i>c, c</i> )	$q^2(\frac{1}{2}p + q)^2 + \frac{\mu}{\sigma^2}[q^2(\frac{1}{2}pb + qc)^2]$
Progeny genotype	Total frequency of occurrence
AA	$p^2 \left[ 1 + \frac{\mu}{\sigma^2} (pa + qb)^2 \right]$
AB	$2pq \left[ 1 + \frac{\mu}{\sigma^2} (pa + qb)(pb + qc) \right]$
BB	$q^2 \left[ 1 + \frac{\mu}{\sigma^2} (pb + qc)^2 \right]$
Total frequency	1

If all genes act additively,  $\sigma_D^2 = D = 0$ , so that

$$\text{cov}(O, O) = \frac{1}{2}\sigma_G^2 \left( 1 + \frac{\mu}{\sigma^2} \sigma_G^2 \right),$$

$$\sigma_{G_1}^2 = \sigma_G^2 \left( 1 + \frac{1}{2} \frac{\mu}{\sigma^2} \sigma_G^2 \right).$$

Summing over loci, and adding the environmental variance to  $\sigma_{G_1}^2$  to give the phenotypic variance of progeny,  $\sigma_1^2$ , we see that then

$$\text{cov}(O, O) = \frac{1}{2}h^2(1 + \mu h^2)\sigma^2,$$

$$\sigma_1^2 = (1 + \frac{1}{2}\mu h^4)\sigma^2,$$

whence the correlation between sibs is

$$r_{OO} = \frac{1}{2}h^2 \frac{1 + \mu h^2}{1 + \frac{1}{2}\mu h^4},$$

which is the formula derived by Reeve (1953).

When dominance deviations are present, however, the occurrence of terms in  $AD$  in  $K_1$  and  $K_2$  implies that assortative mating will introduce correlations between the additive and dominance components of different loci, and also between their dominance components. These correlations will bias the sib-correlation in an unpredictable way, and probably to a serious extent if some of the genes are strongly non-additive in effect and assortative mating is close.

One special case is of interest. If the gene frequencies are all  $\frac{1}{2}$  or close to  $\frac{1}{2}$ , the terms with a factor  $(p - q)$  can be ignored, and then, if  $r_1$  is the correlation



between sibs after assortative mating, compared with  $r$  when mating is at random, we have approximately,

$$r_1 = r \left[ \frac{1 + \mu \left\{ 4r - h^2 \left( \frac{h^2}{2r} \right) \right\}}{1 + \frac{1}{2} \mu h^4} \right],$$

where  $h^2$  is the fraction of the phenotypic variance which is due to additive genetic effects. This again reduces to the formula for additive effects where  $r = \frac{1}{2}h^2$ , but if some dominance is present acting in either direction, then  $r > \frac{1}{2}h^2$  and  $r_1/r$  becomes larger than in the additive case. This gives an example of the kind of bias which assortative mating may introduce into the estimate of the correlation between sibs, when non-additive gene effects are present.

In conclusion, then, it appears that assortative mating, or selection to increase mid-parental variance, will not bias appreciably the regression of offspring on mid-parent, provided that individual gene substitution effects are fairly small, but that more serious bias is likely to arise in the correlation between sibs.

#### 4. SUMMARY

The regression of progeny on mid-parent value is often used in progeny tests to estimate the heritability of a quantitative character. The statistical precision of such an estimate can be considerably increased without increasing the size of the test, by using assortative mating or selection of parents (or both together) so as to increase the mid-parent variance; but the danger arises that this may introduce bias into the estimate through correlation between non-additive gene effects.

It is shown by a mathematical argument that such bias will be negligible provided that all individual gene substitution effects are small compared with the phenotypic standard deviation of the character. Under this condition, deviations from additive effects either within or between loci will not appreciably affect the expected value of the regression on mid-parent, compared with its expected value in a test using random mating.

Correlation between the non-additive gene effects is likely to cause more serious bias to the correlation between sibs, when non-random mating is used.

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