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Assortative mating and artificial selection : a second appraisal

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Summary

The impact on selection response of the positive assortative mating of selected parents was determined for a 2 generation cycle. Relative efficiency refers to the incremental response in the second generation and is defined as the per cent increase in selection response due to mating individuals assortatively instead of randomly. As determined by relative efficiency, assortative mating is most useful when heritability is large, parental selection intensity is low and offspring selection intensity is high. Compared with selection on progeny phenotype, the efficiency of assortative mating is greatly enhanced when progeny are selected on an index incorporating information on parents, the influence being greatest at low heritabilities. Given 10 p. 100 of parents and offspring selected and a heritability of .05, relative efficiency under index selection is 5 p. 100 compared to only .4 p. 100 under mass selection. Over the range of offspring selection intensities considered, relative efficiency under index selection varied between (5-3 p. 100) when heritability equals .05 with 10 p. 100 of parents selected, to (21-15 p. 100) when heritability equals .8 with 90 p. 100 of parents selected.

Key words : Index selection, positive assortative mating, selection.

Résumé

Homogamie et sélection artificielle : une nouvelle évaluation

On a déterminé, pendant un cycle de 2 générations, l'effet, sur la réponse à la sélection, de l'homogamie positive de parents sélectionnés. L'efficacité relative se rapporte à l'accroissement de réponse obtenu chez les descendants issus de la 2^{e} génération : elle est définie comme le pourcentage d'augmentation de la réponse à la sélection due à l'homogamie, comparée à des accouplements au hasard. En terme d'efficacité relative, l'homogamie est surtout utile lorsque l'héritabilité est importante et que l'intensité de sélection est faible chez les reproducteurs de 1re génération, mais élevée chez les reproducteurs de la 2^{e} génération. L'efficacité de l'homogamie est considérablement accrue lorsque les reproducteurs de la 2^{e} génération sont sélectionnés, non pas sur leur phénotype, mais sur un index incorporant l'information relative à leurs parents, surtout si l'héritabilité est faible. Pour un taux de sélection de 10 p. 100 dans les 2 générations et pour une valeur de 0,05 de l'héritabilité, l'efficacité relative est de 5 p. 100 avec une sélection sur index, contre seulement 0,4 p. 100 avec une sélection individuelle. Dans l'intervalle considéré pour les intensités de sélection en 2^{e} génération, l'efficacité relative (avec une sélection sur index) varie de 5-3 p. 100 quand l'héritabilité vaut 0,05 et que le taux de sélection en 1re génération est de 10 p. 100, à 21-15 p. 100 quand l'héritabilité vaut 0,8 et que le taux de sélection en 1re génération est de 90 p. 100.

Mots clés : Sélection sur index, homogamie, sélection.

I. Introduction

McBride and Robertson (1963) showed how selection with positive assortative mating can lead to larger selection response than selection with random mating. In a simulation study, De Lange (1974) concluded that assortative mating is most useful when the trait is polygenic, selection intensity is low and heritability (h^2) high. Baker (1973) studied the effectiveness of assortative mating of selected parents followed by selection of offspring and claimed that in most cases assortative mating will increase selection response in the progeny but by no more than 10 p. 100. When the fraction of parents selected is 20 p. 100 or less, Baker found that assortative mating will increase selection response by no more than 4 or 5 p. 100. Smith & Hammond (1987) questioned these results because :

(1) Assuming selection response proportional to the genotypic standard deviation can result in an underestimate of the relative efficiency of assortative mating by as much as two percentage units.

(2) Departure from normality in the offspring generation should not be assumed negligible when h^2 is high and parents are mated assortatively.

(3) The merit of assortative mating should not be based exclusively on responses possible under mass selection. The efficiency of assortative mating might be substantially different when index selection, incorporating information on relatives, is used.

Implicit assumptions questioned by the first two points are sometimes reasonable. However, care is required when the error resulting from an approximation approaches the same order of magnitude as the quantity (e.g., relative efficiency) being estimated. The third point has the potential of being a serious objection as the fundamental reason for assortative mating may be to arrange future pedigree information. The purpose of this paper to rework Baker's analysis accounting for the above points.

II. Materials and methods

We concern ourselves with analytical evaluation of responses to selection after 1 and 2 generations. In the first generation unrelated individuals (parents) were selected by mass culling on a single phenotypic expression. To produce the second generation parents were either mated randomly or assortatively. Comparing selection responses in the second generation allowed determination of the efficiency of assortative mating over random mating. This was done for two types of selection in the second generation ; mass selection on a single phenotype, and index selection using parental phenotypes as well as the progeny phenotype.

Our analysis depends on a series of assumptions that are described next.

A. *Assumptions*

Phenotypes and genotypes are multivariate normal random variables. Further, genotypes are inherited additively and genotype by environment interactions do not exist. The usual companion clause to these assumptions is that genotypes are expressed as the sum of small effects over a large number of additive and unlinked loci. This allows the depiction of genotypes as normal random variables. BAKER (1973) used normal approximations and presented results as a function of loci number. Our analysis differs from that of BAKER in that results are not presented as a function of loci number. We have simply assumed that there are enough loci for normality to hold.

Populations were assumed to be of infinite size so as to allow easy calculation of selection responses. Similar calculations for finite populations are complicated and would require consideration of order statistics. The results of BAKER (1973) were not a function of population size.

The population was in linkage equilibrium prior to the selection of first generation animals. That is, there were no asymmetries caused by prior selection. BAKER (1973) implicity made this assumption and allowed a reduction in variance due to selection in generation 1. We accommodated both the reduction in variance and departure from normality. Though it is difficult theoretically, it would be desirable to extend our analysis beyond 2 generations.

B. *Calculating selection response*

To calculate selection response, (co)variances were needed for all measures used as culling criterion and the metric for which selection response applies. For two generations of mass selection, these measures are parental phenotypes (P_1 and P_2 where the subscripts define the sex), offspring phenotype (P_o) and offspring additive merit (A_o). Given mass selection in generation one and index selection in generation two, a further measure, I, which is the index that predicts A_o from P_1, P_2 and P_o, was required. The specified (co)variances correspond to populations where no selection occurs and when parents are mated assortatively or randomly. Once population parameters were defined, truncated multivariate normal theory (BIRNBAUM & MEYER, 1953 ; TALLIS, 1961) allowed the calculation of exact selection response. Hence, we have modelled the phenomenon that additive genetic variance decreases with selection and increases with positive assortative mating. As we dealt with a multivariate system we were also able to assess the importance of prearranging P_1 and P_2 when selecting progeny from an Index, I.

1. *Random mating*

Under random mating the (co)variance structure for P_1, P_2, P_o, I and A_o is :

$$\begin{bmatrix} 1 & 0 & 1/2\,h^2 & w_1 + 1/2\,h^2 w_2 & 1/2\,h^2 \\ & 1 & 1/2\,h^2 & w_1 + 1/2\,h^2 w_2 & 1/2\,h^2 \\ & & 1 & h^2 w_1 + w_2 & h^2 \\ & \text{symmetric} & & h^2 (w_1 + w_2) & h^2 (w_1 + w_2) \\ & & & & h^2 \end{bmatrix}$$

where the phenotypic variance has been standardized to 1 and w_1 and w_2 are weights in the selection index, $I = w_1 (P_1 + P_2) + w_2 P_o$, for which w_1 is given as $h^2 (1 - h^2)/(2 - h^4)$

and w_2 is given as $h^2(2 - h^2)/(2 - h^4)$. The weights of the selection index are unaffected by selection in generation one.

The first moments of P_1, P_2, P_o, I and A_o are taken, with no loss in generality, to be null. Selection in the first generation was cast as truncating P_1 and P_2 above some threshold (t_1). The same selection intensity in both sexes was used so as to be consistent with BAKER (1973). Selection in the second generation is cast as truncating P_o (or I) above a threshold (t_2). To evaluate selection response, the expectation of A_o given truncation on P_1, P_2 and P_o (or I) was computed. This expectation is denoted by $E[A_o|P_1 > t_1, P_2 > t_1, P_o \text{ (or I)} > t_2]$.

Explicit representation of selection response requires the following definitions :

(1) Standard normal density,

$$Z(x) = (2\pi)^{-1/2} \exp(-1/2x^2), \; -\infty < x < \infty \; ;$$

(2) Standard univariate normal area,

$$U(t) = \Pr[X > t]$$

where Pr [A] is the probability of event A and X is standard normal ;

(3) Standard bivariate normal volume,

$$B(c_1, c_2, r) = \Pr[X_1 > c_1, X_2 > c_2]$$

where X_1 and X_2 are standard bivariate normal with correlation r ;

(4) Standardized yet specific trivariate normal space,

$$T(c_p, c_o, r) = \Pr[X_1 > c_p, X_2 > c_p, X_3 > c_o]$$

where X_1, X_2 and X_3 are trivariate normal with moments

$$E\begin{bmatrix} X_1 \\ X_2 \\ X_3 \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix} \quad \text{and var} \begin{bmatrix} X_1 \\ X_2 \\ X_3 \end{bmatrix} = \begin{bmatrix} 1 & 0 & r \\ 0 & 1 & r \\ r & r & 1 \end{bmatrix}.$$

A routine MDBNOR, from IMSL (International Mathematical and Statistical Librairies, Inc.) was used to evaluate $B(c_1, c_2, r)$. A routine was written for evaluating $T(c_p, c_o, r)$, based on a tetrachoric series described by KENDALL (1941). The common view is that this series converges slowly for large $|r|$. However, in our analysis $|r|$ is never larger than .493 which is considerably less than the theoretical maximum, .707. Tests showed that our routine performed well when $r = .493$. Other useful methods of evaluating $T(c_p, c_o, r)$ can be derived by applying suggestions of FOULLEY & GIANOLA (1984) and RUSSELL *et al.* (1985).

The theory of BIRNBAUM & MEYER (1953) and TALLIS (1961) indicates that, under mass selection of progeny,

$E[A_o|P_1 > t_1, P_2 > t_1, P_o > t_2]$ equals

$$\frac{h^2 Z(t_1) B(t_1, t_{21}, r) + h^2 Z(t_2) B(t_{12}, t_{12}, s)}{T(t_1, t_2, q)} \qquad (1)$$

where

$q = 1/2\ h^2$

$t_{21} = (t_2 - qt_1)/(1 - q^2)^{1/2}$,

$t_{12} = (t_1 - qt_2)/(1 - q^2)^{1/2}$,

$r = q/(1 - q^2)^{1/2}$ and

$s = - q^2/(1 - q^2)$.

Note that (1) is a generalization of the well known formula, $ih^2\sigma_p$ (i = selection intensity, σ_p standardized to 1 herein), which estimates selection response after 1 generation of mass selection.

Likewise, under index selection of progeny,

$$E\ [A_o|P_1 > t_1,\ P_2 > t_1,\ I > t_2] = E\ [A_o|P_1 > t_1,\ P_2 > t_1,\ I_\# > t_\#] \qquad (2)$$

where $I_\# = I/h\ (w_1 + w_2)^{1/2}$ and $t_\# = t_2/h\ (w_1 + w_2)^{1/2}$, and consequently (2) equals

$$\frac{h^2 Z\ (t_1)\ B\ (t_1,\ t_{\#1},\ r) + h\ (w_1 + w_2)^{1/2}\ Z\ (t_\#)\ B\ (t_{1\#},\ t_{1\#},\ s)}{T\ (t_1,\ t_\#,\ q)} \qquad (3)$$

where

$q = (w_1 + 1/2\ h^2w_2)/\{h\ (w_1 + w_2)^{1/2}\}$,

$t_{\#1} = (t_\# - qt_1)/(1 - q^2)^{1/2}$,

$t_{1\#} = (t_1 - qt_\#)/(1 - q^2)^{1/2}$,

$r = q/(1 - q^2)^{1/2}$ and

$s = - q^2/(1 - q^2)$.

We needed $(t_1,\ t_2)$ or alternatively $(t_1,\ t_\#)$ to evaluate (1) or (3). Truncation points were determinated given the proportion of parents selected (S_p) and the proportion of progeny selected (S_o). Infinite population size implies

$$U\ (t_1) = S_p \qquad (4)$$

for t_1 in (1) or (3) and

$$T\ (t_1,\ t,\ q) = S_p \cdot S_p \cdot S_o \qquad (5)$$

where

$t = t_2$, $q = 1/2\ h^2$ in (1) or

$t = t_\#$, $q = (w_1 + 1/2\ h^2w_2)/\{h\ (w_1 + w_2)^{1/2}\}$ in (3).

Truncation point t_1 was computed from (4) via Newtons method, that is the iterative scheme

$$t_1^{k+1} = t_1^k + \{U\ (t_1^k) - S_p\}/Z\ (t_1^k) \qquad (6)$$

where t_1^o is some starting value and for sufficiently large i, $t_1 = t_1^i$. After t_1 was determined, t was found in (5) by Newtons method again, that is

$t^{k+1} = t^k + \{T\ (t_1,\ t^k,\ q) - S_p{\cdot}S_p{\cdot}S_o\}/\{Z\ (t^k)\ B\ (a,\ a,\ s)\}$,

$a = (t_1 - qt^k)/(1 - q^2)^{1/2}$,

$s = - q^2/(1 - q^2)$,

where t^o is some starting value and for sufficiently large i, $t = t^i$. A good starting value proved to be :

$$t^o = 2qZ\,(t_1)/S_p + t^*\,[1 - 2q^2V\,(t_1)]^{1/2}$$

where t^* is defined implicitly but $U\,(t^*) = S_o$ and

$$V\,(t_1) = \{Z\,(t_1)/S_p\}\,\{Z\,(t_1)/S_p - t_1\}$$

2. *Assortative mating*

There are no conceptual difficulties in allowing assortative mating prior to selection in generation one. We can describe selection of parents as selection of mating pairs, so that if one parent is selected the preassigned mate is selected as well. Selection followed by mating is mathematically equivalent to mating followed by selection. This property allowed us to compute selection response under assortative mating via the theory of truncated multivariate normal. This is not possible if selection intensities are different for each sex, nor is it possible for negative assortative mating.

Define A_1 and A_2 as the additive genetic component of P_1 and P_2, respectively. The (co)variance structure of P_1, P_2, A_1, A_2, P_o and A_o under assortative mating with no selection was determined as

$$\begin{bmatrix} 1 & 1 & h^2 & h^2 & h^2 & h^2 \\ & 1 & h^2 & h^2 & h^2 & h^2 \\ & & h^2 & h^4 & 1/2\,h^2\,(1+h^2) & 1/2\,h^2\,(1+h^2) \\ \text{symmetric} & & & h^2 & 1/2\,h^2\,(1+h^2) & 1/2\,h^2\,(1+h^2) \\ & & & & 1 + 1/2\,h^4 & h^2 + 1/2\,h^4 \\ & & & & & h^2 + 1/2\,h^4 \end{bmatrix} \qquad (7)$$

using the following reasoning : positive assortative mating in an infinite population implies that the phenotypic correlation among mates is one. Thus, the above matrix is singular. Principals of conditional covariance allowed determination of other elements in (7). For example,

$$\begin{aligned} \text{Cov}\,(P_1,\ A_2) &= \text{Cov}\,\{E\,(P_1|P_2),\ E\,(A_2|P_2)\} + E\,\{\text{Cov}\,(P_1,\ A_2|P_2)\} \\ &= \text{Cov}\,\{P_2,\ h^2P_2\} + E\,\{0\} \\ &= h^2 \end{aligned}$$

and

$$\begin{aligned} \text{Cov}\,(A_1,\ A_2) &= \text{Cov}\,\{E\,(A_1|P_1),\ E\,(A_2|P_1)\} + E\,\{\text{Cov}\,(A_1,\ A_2|P_1)\} \\ &= \text{Cov}\,\{h^2\,P_1,\ h^2P_1\} + E\,\{0\} \\ &= h^4 \end{aligned}$$

Consider the selection index used to predict A_o given P_1, P_2 and P_o. This index can be derived from (7), yet we know that the weights are unaffected by mating in generation one. Thus, the weights given previously for random mating apply (i.e., $I = w_1\,(P_1 + P_2) + w_2P_o$). Using (7), the (co)variance structure of P_1, P_2, P_o, I and A_o is :

$$\begin{bmatrix} 1 & 1 & h^2 & 2w_1 + h^2w_2 & h^2 \\ & 1 & h^2 & 2w_1 + h^2w_2 & h^2 \\ \text{symmetric} & & 1 + 1/2\ h^4 & 2w_1h^2 + (1 + 1/2\ h^4)w_2 & h^2 + 1/2\ h^4 \\ & & & h^2\ (2w_1 + (1 + 1/2\ h^2)w_2) & h^2\ (2w_1 + (1 + 1/2\ h^2)w_2) \\ & & & & h^2 + 1/2\ h^4 \end{bmatrix} \quad (8)$$

Computation of selection response from (8), is simplified by noting that $P_2 > t_1$ is redundant information given that $P_1 > t_1$. Hence,

$E\ [A_o|P_1 > t_1,\ P_2 > t_1,\ P_o \text{ (or I)} > t_2] = E\ [A_o|P_1 > t_1,\ P_o \text{ (or I)} > t_2]$

The selection response from mass selection is given by :

$$E\ [A_o|P_1 > t_1,\ P_o > t_2] = E\ [A_o|P_1 > t_1,\ P_\# > t_\#] \qquad (9)$$

where $P_\# = P_o/(1 + 1/2\ h^4)^{1/2}$ and $t_\# = t_2/(1 + 1/2\ h^4)^{1/2}$. To evaluate (9) we applied the methods of BIRNBAUM & MEYER (1953) & TALLIS (1961) to give :

$$\frac{h^2Z\ (t_1)\ U\ (t_{\#1}) + (h^2 + 1/2\ h^4)/(1 + 1/2\ h^4)^{1/2}\ Z\ (t_\#)\ U\ (t_{1\#})}{B\ (t_1,\ t_\#,\ q)} \qquad (10)$$

where :

$q\ = h^2/(1 + 1/2\ h^4)^{1/2}$,

$t_{\#1} = (t_\# - qt_1)/(1 - q^2)^{1/2}$ and

$t_{1\#} = (t_1 - qt_\#)/(1 - q^2)^{1/2}$

The selection response from index selection is given by :

$$E\ [A_o|P_1 > t_1,\ I > t_2] = E\ [A_o|P_1 > t_1,\ I_\# > t_\#] \qquad (11)$$

where $I_\# = I/[h^2\ (2w_1 + (1 + 1/2\ h^2)\ w_2)^{1/2}$ and $t_\# = t_2/[h(2w_1 + (1 + 1/2\ h^2)\ w_2)^{1/2}]$. Expectation (11) was calculated as :

$$\frac{h^2\ Z\ (t_1)\ U\ (t_{\#1}) + h\ \{2w_1 + (1 + 1/2\ h^2)\ w_2\}^{1/2}\ Z\ (t_\#)\ U\ (t_{1\#})}{B\ (t_1,\ t_\#,\ q)} \qquad (12)$$

where :

$q\ = (2w_1 + h^2w_2)/[h\ \{2w_1 + (1 + 1/2\ h^2)\ w_2\}^{1/2}]$

$t_{\#1} = (t_\# - qt_1)/(1 - q^2)^{1/2}$ and

$t_{1\#} = (t_1 - qt_\#)/(1 - q^2)^{1/2}$.

In evaluating (10) or (12) we needed t_1 and $t_\#$. Truncation point t_1 was obtained from the analysis described for random mating. $t_\#$ was obtained by solving

$$B\ (t_1,\ t_\#,\ q) = S_o \cdot S_p \qquad (13)$$

given t_1. Equation (13) was solved by Newtons method, that is the iterative scheme

$t_\#^{k+1} = t_\#^k + \{B\ (t_1,\ t_\#^k,\ q) - S_o \cdot S_p\}/\{Z\ (t_\#^k)\ U\ (a)\}$,

$a = (t_1 - qt_\#^k)/(1 - q^2)^{1/2}$,

where $t^o_{\#}$ is some starting value and for sufficiently large i, $t_{\#} = t^i_{\#}$. The starting value used was :

$$t^o_{\#} = qZ(t_1)/S_p + t^* [1 - q^2 V(t_1)]^{1/2}$$

C. *Relative efficiency*

Baker (1973) reported the relative increase in genotypic variance in generation two, following selection and assortative mating in generation one. For comparison we examined the deviation of selection response between the second and the initial generations. The initial selection response was calculated as

$$h^2 Z(t_1)/U(t_1)$$

where t_1 was defined by (4) and calculated by scheme (6).

Under mass and index selection, relative efficiency (p. 100) was calculated as

$$RE = 100 \{(DRA/DRR) - 1\} \tag{14}$$

where DRA is the deviated response due to selection with assortative mating and DRR is the deviated response due to selection with random mating. Relative efficiency was calculated for a range of h^2, S_p and S_o.

D. *Departure from normality*

We have argued that departure from normality should not be ignored when calculating relative efficiency. Even if normality is a tenable assumption there is no harm done in allowing for the possibility that normality does not hold. Alternatively, Bulmer (1980, p. 154) argues that departure from normality induced by selection can be safely ignored.

The effect of departure from normality was investigated only for mass selection. The effect was not considered with index selection as few would deny the lack of normality displayed by I after truncating on P_1 and P_2.

Relative efficiency, DRA and DRR was recomputed assuming normality in the offspring. We use the subscripts 1 and 2 to indicate how the above quantities were computed ; RE_1, DRA_1 and DRR_1 evaluated correctly and RE_2, DRA_2 and DRR_2 evaluated under conditions of normality. Precisely, DRA_2 and DRR_2 were evaluated as

$$i\, \sigma^2_a/\sigma_p \tag{15}$$

where $i = Z(t^*)/S_o$, and for DRA_2

$$\sigma^2_a = h^2 + 1/2\, h^4 - h^4 V(t_1)$$

$$\sigma_p = [1 + 1/2\, h^4 - h^4 V(t_1)]^{1/2},$$

for DRR_2

$$\sigma^2_a = h^2 - 1/2\, h^4 V(t_1)$$

$$\sigma_p = [1 - 1/2\, h^4 V(t_1)]^{1/2}.$$

The quantity, RE_2, was calculated from (14) using DRA_2 and DRR_2. Inspection of (14) and (15) shows that RE_2 is independent of i or S_o.

Error terms (p. 100) for DRA_2 and DRR_2 were calculated as :

$E_1 = 100\,(DRA_1/DRA_2 - 1)$

$E_2 = 100\,(DRR_1/DRR_2 - 1)$

These percentages will be reported rather than DRA_1, DRA_2, DRR_1 and DRR_2.

III. Results and discussion

A. *Mass selection*

1. *Relative efficiency*

Relative efficiencies under mass selection are presented in table 1. These quantities varied between 0.41 p. 100 ($h^2 = .05$, $S_p = .1$, $S_o = .9$) and 20.98 p. 100 ($h^2 = .8$, $S_p = .9$, $S_o = .1$). Our results support De Lange (1974) in that assortative mating was found to be most effective when h^2 was high and when the parental selection intensity was low. Differences in RE as a function of S_o, holding h^2 and S_p constant, were attributed to departure from normality, which is discussed in the next section.

Relative efficiencies calculated assuming normality are displayed in table 2 and are, on the whole, slightly larger than what Baker (1973) predicted. The primary reason for the discrepancy seems to be due to Baker's assumption that selection response was proportional to the genotypic standard deviation. To overcome this we use a set of ratios defined by Baker as :

$$\frac{\text{Genotypic variance in progeny of assortatively mated parents}}{\text{Genotypic variance in progeny of randomly mated parents}}$$

Any particular ratio (R) was a function of h^2, parental selection intensity, loci number and initial gene frequency. This ratio was translated into a RE using :

$100\,[R/\{h^2\,(R - 1) + 1\}^{1/2} - 1]$

If we consider $S_p = .2$, $h^2 = .2$, 100 loci and gene frequency $= .5$, Baker's corrected RE becomes 2.1. The analogous figure listed in table 2 is 2.15. If we consider $S_p = .2$, $h^2 = .8$, 100 loci and gene frequency $= .5$, Baker's corrected RE is 7.6. The corresponding value in table 2 is 7.81.

2. *Departure from normality*

Under conditions of normality in the offspring generation, relative efficiencies for the 2 generation cycle are independent of S_o and are listed in table 2. However, the effect of departure from normality on RE appears uniform in table 1 ; RE is enhanced for low S_o, holding h^2 and S_p constant. The influence of departure from normality on RE can be characterized by comparing tables 1 and 2. For example, when $S_p = .1$ and $h^2 = .05$ the RE calculated under conditions of normality is .42 (table 2). This value agrees well with the 7 analogous figures in table 1 because departure from normality is slight. Alternatively, if we take $S_p = .2$ and $h^2 = .8$ the RE in table 2 is 7.81. This number is intermediate among the 7 analogous numbers in table 1 as there is appreciable non-normality in the offspring. Departure from normality appears most

TABLE 1

Relative efficiency (p. 100) of assortative mating over random mating after 2 generations of mass selection.

Proportion of parents selected	Heritability	Proportion of offspring selected						
		.1	.2	.4	.5	.6	.8	.9
.1	.05	0.43	0.43	0.42	0.42	0.42	0.41	0.41
	.10	0.89	0.87	0.85	0.84	0.83	0.81	0.79
	.20	1.85	1.78	1.70	1.66	1.63	1.55	1.50
	.40	4.01	3.73	3.39	3.26	3.13	2.86	2.67
	.60	6.38	5.75	5.01	4.73	4.47	3.93	3.58
	.80	8.63	7.58	6.39	5.94	5.54	4.72	4.21
.2	.05	0.56	0.55	0.55	0.54	0.54	0.53	0.53
	.10	1.14	1.12	1.09	1.08	1.07	1.04	1.02
	.20	2.39	2.30	2.18	2.14	2.09	1.99	1.92
	.40	5.13	4.76	4.32	4.15	3.98	3.62	3.38
	.60	8.05	7.26	6.32	5.96	5.62	4.92	4.47
	.80	10.70	9.44	7.96	7.40	6.88	5.84	5.19
.4	.05	0.80	0.79	0.78	0.77	0.77	0.76	0.75
	.10	1.62	1.59	1.55	1.53	1.52	1.48	1.45
	.20	3.37	3.24	3.08	3.01	2.95	2.80	2.70
	.40	7.10	6.61	6.00	5.76	5.53	5.02	4.67
	.60	10.86	9.85	8.62	8.13	7.67	6.70	6.07
	.80	13.97	12.50	10.65	9.92	9.24	7.83	6.94
.5	.05	0.93	0.92	0.91	0.90	0.89	0.88	0.87
	.10	1.89	1.85	1.80	1.78	1.76	1.72	1.68
	.20	3.89	3.75	3.57	3.49	3.41	3.25	3.12
	.40	8.11	7.57	6.90	6.62	6.36	5.78	5.38
	.60	12.21	11.15	9.81	9.27	8.76	7.66	6.93
	.80	15.45	13.96	12.02	11.22	10.47	8.90	7.88
.6	.05	1.07	1.06	1.05	1.04	1.04	1.03	1.02
	.10	2.18	2.14	2.09	2.06	2.04	1.99	1.95
	.20	4.47	4.32	4.11	4.03	3.94	3.75	3.62
	.40	9.19	8.62	7.89	7.58	7.29	6.64	6.19
	.60	13.60	12.52	11.11	10.53	9.96	8.74	7.92
	.80	16.89	15.46	13.47	12.63	11.82	10.09	8.95
.8	.05	1.47	1.46	1.44	1.44	1.43	1.41	1.40
	.10	2.96	2.91	2.85	2.83	2.80	2.74	2.69
	.20	5.96	5.79	5.56	5.46	5.36	5.14	4.97
	.40	11.74	11.18	10.41	10.08	9.75	8.98	8.43
	.60	16.56	15.65	14.30	13.69	13.08	11.67	10.67
	.80	19.68	18.63	16.92	16.10	15.26	13.31	11.92
.9	.05	1.78	1.77	1.75	1.75	1.74	1.73	1.71
	.10	3.56	3.51	3.45	3.43	3.40	3.34	3.30
	.20	7.04	6.88	6.67	6.58	6.48	6.26	6.09
	.40	13.36	12.91	12.25	11.95	11.64	10.89	10.32
	.60	18.17	17.53	16.47	15.96	15.41	14.06	13.01
	.80	20.98	20.34	19.13	18.48	17.77	15.93	14.48

TABLE 2

Relative efficiency (p. 100) of assortative mating over random mating after 2 generations of mass selection. Calculations assume normality in second generation.

Proportion of parents selected	Heritability					
	.05	.10	.20	.40	.60	.80
.1	.42	.84	1.67	3.31	4.90	6.28
.2	.54	1.08	2.15	4.22	6.16	7.81
.4	.77	1.54	3.02	5.84	8.37	10.36
.5	.90	1.78	3.50	6.71	9.50	11.63
.6	1.04	2.07	4.04	7.66	10.72	12.96
.8	1.44	2.83	5.47	10.10	13.71	16.10
.9	1.75	3.43	6.57	11.90	15.80	18.19

influential when h^2 is large. In fact, for h^2 of .6 or .8, errors induced by assuming normality in the offspring are the same order of magnitude as RE itself.

A better understanding of the effect of departure from normality on RE is possible by considering the component error terms, E_1 and E_2, displayed in table 3. Values in tables 3 and 2 are related to values in table 1 by the mathematical relationship :

$$(100 + RE_1) = (100 + RE_2)\,(100 + E_1)/(100 + E_2) \qquad (16)$$

From (16) we see that E_1 and E_2 work in opposite directions and in particular when $E_1 = E_2$ we have $RE_1 = RE_2$. The terms E_1 and E_2 generally have the same sign in table 3. Thus, E_1 and E_2 cancel partially in (16). Nevertheless, for all pairs (E_1, E_2) found in table 3 the absolute value of E_2 is greater than the absolute value of E_1. Consequently, the effect of departure from normality on RE is notable when either E_1 or E_2 are different from zero.

In table 3 E_1 and E_2 are small when S_0 is in the .4 to .6 range. Both E_1 and E_2 become notably positive as S_0 approaches .1. The error terms become notably negative as S_0 approaches .9. These observations are consistent with the fact that values of RE in table 2 are similar to those in table 1 when S_0 is intermediate (eg, $S_0 = .5$). Descrepancies occur in tables 1 and 2 when S_0 approaches .1 or .9.

There are some patterns in table 3 worth listing ; error terms grow as h^2 increases, error terms are larger when parents are mated assortatively (ie, $|E_1| > |E_2|$), and error terms are largest when S_p is .5, .6 or .8 (ie, when the parental selection intensity is low or intermediate).

The last observation is easily explained. Let x and y be correlated normal variables with respective means equalling zero. We can represent x by

$$x = by + e \qquad (17)$$

where b is the regression of x on y and e is a residual that is uncorrelated with y. If y is truncated departure from normality exists with respect to y. However, the variance of y decreases and from (17) we see that e can dominate x if the variance of y becomes very small. With heavy truncation on y the variance of y approaches zero and x becomes normal because e is normal. Alternatively, with no truncation, x is normal by definition.

TABLE 3

Error (p. 100) [(a)] *from assuming normality when calculating selection response for progeny of selected parents when the parents are mated assortatively (at random).*

Proportion of parents selected	Heritability	Proportion of offspring selected			
		.1	.4	.6	.9
.1	.05	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	.10	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	− 0.1 (0.0)
	.20	0.2 (0.1)	0.0 (0.0)	− 0.1 (0.0)	− 0.2 (− 0.1)
	.40	0.9 (0.2)	0.1 (0.0)	− 0.2 (− 0.1)	− 0.8 (− 0.2)
	.60	2.0 (0.5)	0.2 (0.1)	− 0.5 (− 0.1)	− 1.7 (− 0.5)
	.80	3.1 (0.9)	0.2 (0.1)	− 0.9 (− 0.2)	− 2.8 (− 0.8)
.2	.05	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	.10	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	− 0.1 (0.0)
	.20	0.3 (0.1)	0.1 (0.0)	− 0.1 (0.0)	− 0.3 (− 0.1)
	.40	1.2 (0.3)	0.2 (0.1)	− 0.3 (− 0.1)	− 1.1 (− 0.3)
	.60	2.5 (0.7)	0.2 (0.1)	− 0.7 (− 0.2)	− 2.2 (− 0.7)
	.80	3.9 (1.2)	0.3 (0.2)	− 1.2 (− 0.3)	− 3.5 (− 1.1)
.4	.05	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	.10	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	− 0.1 (0.0)
	.20	0.4 (0.1)	0.1 (0.0)	− 0.1 (0.0)	− 0.4 (− 0.1)
	.40	1.6 (0.4)	0.2 (0.1)	− 0.4 (− 0.1)	− 1.5 (− 0.4)
	.60	3.3 (1.0)	0.4 (0.1)	− 0.9 (− 0.2)	− 3.0 (− 0.9)
	.80	4.9 (1.6)	0.5 (0.2)	− 1.4 (− 0.4)	− 4.5 (− 1.5)
.5	.05	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	.10	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	− 0.1 (0.0)
	.20	0.5 (0.1)	0.1 (0.0)	− 0.1 (0.0)	− 0.5 (− 0.1)
	.40	1.8 (0.5)	0.3 (0.1)	− 0.4 (− 0.1)	− 1.7 (− 0.5)
	.60	3.6 (1.1)	0.5 (0.2)	− 0.9 (− 0.2)	− 3.3 (− 1.0)
	.80	5.2 (1.7)	0.6 (0.3)	− 1.4 (− 0.4)	− 5.0 (− 1.7)
.6	.05	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	.10	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	− 0.1 (0.0)
	.20	0.6 (0.1)	0.1 (0.0)	− 0.1 (0.0)	− 0.6 (− 0.1)
	.40	2.0 (0.6)	0.3 (0.1)	− 0.5 (− 0.1)	− 1.9 (− 0.5)
	.60	3.8 (1.2)	0.5 (0.2)	− 0.9 (− 0.3)	− 3.6 (− 1.1)
	.80	5.4 (1.8)	0.7 (0.3)	− 1.4 (− 0.4)	− 5.3 (− 1.8)
.8	.05	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	.10	0.2 (0.0)	0.0 (0.0)	0.0 (0.0)	− 0.2 (0.0)
	.20	0.6 (0.2)	0.1 (0.0)	− 0.1 (0.0)	− 0.6 (− 0.2)
	.40	2.1 (0.6)	0.4 (0.1)	− 0.4 (− 0.1)	− 2.1 (− 0.6)
	.60	3.8 (1.3)	0.8 (0.2)	− 0.8 (− 0.3)	− 3.9 (− 1.3)
	.80	5.0 (1.9)	1.1 (0.4)	− 1.1 (− 0.4)	− 5.5 (− 1.9)
.9	.05	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	− 0.1 (0.0)
	.10	0.2 (0.0)	0.0 (0.0)	0.0 (0.0)	− 0.2 (0.0)
	.20	0.6 (0.2)	0.1 (0.0)	− 0.1 (0.0)	− 0.6 (− 0.2)
	.40	1.9 (0.6)	0.4 (0.1)	− 0.3 (− 0.1)	− 2.0 (− 0.6)
	.60	3.2 (1.1)	0.8 (0.3)	− 0.5 (− 0.2)	− 3.6 (− 1.2)
	.80	4.0 (1.6)	1.2 (0.4)	− 0.6 (− 0.3)	− 4.8 (− 1.8)

(a) Calculated as : 100 (actual/approximate − 1).

TABLE 4

Relative efficiency (p. 100) of assortative mating over random mating after an initial generation of mass selection followed by one generation of index selection.

Proportion of parents selected	Heritability	Proportion of offspring selected						
		.1	.2	.4	.5	.6	.8	.9
.1	.05	5.34	4.75	4.08	3.82	3.59	3.12	2.82
	.10	5.60	4.97	4.26	3.99	3.74	3.24	2.92
	.20	6.13	5.42	4.62	4.32	4.04	3.48	3.13
	.40	7.23	6.36	5.36	4.99	4.65	3.97	3.55
	.60	8.34	7.29	6.10	5.65	5.25	4.45	3.96
	.80	9.32	8.11	6.74	6.23	5.77	4.86	4.30
.2	.05	6.71	5.99	5.14	4.81	4.51	3.90	3.51
	.10	7.03	6.26	5.35	5.01	4.69	4.05	3.64
	.20	7.67	6.81	5.80	5.41	5.06	4.34	3.89
	.40	8.99	7.94	6.70	6.23	5.80	4.93	4.39
	.60	10.30	9.05	7.58	7.03	6.52	5.50	4.87
	.80	11.44	10.02	8.35	7.71	7.14	5.98	5.27
.4	.05	8.98	8.10	7.00	6.57	6.16	5.32	4.77
	.10	9.38	8.45	7.29	6.83	6.40	5.51	4.94
	.20	10.18	9.15	7.86	7.35	6.88	5.89	5.26
	.40	11.79	10.56	9.02	8.40	7.83	6.65	5.90
	.60	13.34	11.93	10.13	9.41	8.74	7.37	6.50
	.80	14.67	13.10	11.08	10.28	9.52	7.98	7.01
.5	.05	10.07	9.15	7.97	7.49	7.04	6.08	5.46
	.10	10.50	9.53	8.29	7.78	7.31	6.30	5.64
	.20	11.35	10.30	8.92	8.37	7.84	6.73	6.01
	.40	13.07	11.83	10.20	9.53	8.90	7.57	6.72
	.60	14.71	13.30	11.42	10.64	9.91	8.37	7.39
	.80	16.10	14.55	12.45	11.59	10.76	9.04	7.94
.6	.05	11.17	10.25	9.03	8.51	8.02	6.95	6.25
	.10	11.62	10.67	9.37	8.83	8.31	7.19	6.45
	.20	12.53	11.49	10.07	9.48	8.91	7.67	6.86
	.40	14.33	13.13	11.47	10.76	10.08	8.61	7.65
	.60	16.04	14.70	12.79	11.98	11.19	9.50	8.39
	.80	17.46	16.01	13.91	13.00	12.12	10.23	9.00
.8	.05	13.48	12.75	11.62	11.10	10.57	9.34	8.46
	.10	13.98	13.22	12.04	11.49	10.94	9.65	8.73
	.20	14.95	14.15	12.88	12.28	11.67	10.26	9.25
	.40	16.84	15.96	14.51	13.82	13.11	11.45	10.26
	.60	18.59	17.64	16.04	15.26	14.45	12.55	11.19
	.80	20.01	19.02	17.30	16.45	15.56	13.45	11.95
.9	.05	14.73	14.24	13.39	12.96	12.49	11.31	10.39
	.10	15.22	14.73	13.85	13.39	12.91	11.67	10.71
	.20	16.20	15.68	14.75	14.26	13.73	12.39	11.34
	.40	18.08	17.53	16.50	15.95	15.34	13.77	12.54
	.60	19.78	19.21	18.10	17.49	16.82	15.04	13.63
	.80	21.15	20.57	19.41	18.76	18.03	16.08	14.52

B. *Index Selection*

Relative efficiencies of assortative mating with index selection are displayed in table 4. These quantities varied between 2.82 p. 100 ($h^2 = .05$, $S_p = .1$, $S_o = .9$) and 21.15 p. 100 ($h^2 = .8$, $S_p = .9$, $S_o = .1$). Like mass selection, assortative mating was found to be most effective when h^2 was high and when S_p was high. However, RE computed under index selection was appreciably larger than the analogous value for mass selection. Fifty nine per cent of the results listed in table 4 are larger than 8 p. 100. This compares with 28 p. 100 in table 1. The differences in RE between mass and index selection was largest when h^2 was small, and was slight when h^2 was large. This result was entirely expected because selection response after 2 generations equals the expectation of I conditional on selection and when h^2 becomes small the relative contributions of P_1 and P_2 to I increase. Alternatively, when h^2 becomes large I approaches P_0 and index selection becomes equivalent to mass selection.

Larger departure from normality in the distribution of I than in the distribution of P_0 was also expected due to the part-whole relationship between I and (P_1, P_2). Indeed, differences in relative efficiencies are larger in table 4 than in table 1, holding h^2 and S_p constant. As with mass selection, RE was enhanced for low S_o. This effect appears to increase with increasing h^2.

IV. Conclusion

Despite a slight underevaluation of assortative mating, BAKER (1973) was generally correct with the assessment that under mass selection assortative mating will increase selection response in progeny but by no more than 10 p. 100 in most situations (BAKER considered cases only were $S_p \leq .5$). However, when h^2 is large and S_p is greater than .5, RE can be larger than 10 p. 100.

Assortative mating under index selection can increase selection response in progeny. Relative efficiency is notably larger than under mass selection. This enhancement is due to the direct use of preassorted information in I.

With regard to RE of assortative mating, we expect different selection indexes to have different properties. Using an index that incorporates prearranged information can enhance RE even if the prior act of arranging mates was unsuccessful in increasing genetic variance. To show this consider the hypothetical case where unselected parents are allowed to mate randomly or assortatively. There are now closed form expressions for RE ; with mass selection of progeny

$$RE = 100\,[(1 + 1/2\,h^2)/(1 + 1/2\,h^4)^{1/2} - 1] \tag{18}$$

and when progeny are selected on I

$$RE = 100\,\{[1 + (1 - 1/2\,h^4)/(3 - 2\,h^2)]^{1/2} - 1\} \tag{19}$$

When h^2 equals 1, (18) and (19) are both equal to 22.47 p. 100. However, as h^2 tends to 0 (18) tends to 0 p. 100 and (19) becomes 15.47 p. 100. Indeed, (19) is never smaller than 15.47 p. 100 which is close to the upper bound. When h^2 is close to 0 assortative mating will show no advantage with mass selection because assortative mating will do little to increase genetic variance. Yet from (19) we see that assortative mating can enhance relative selection response even though the magnitude of this response is small. Note that this effect is specifically related to using prearranged pedigree information. It is not an effect expected from using an index constructed from information on collateral relatives, i.e. when prearranged information is not used.

There is a further effect that various types of index selection may have on the value of assortative mating. If animals are mated assortatively by an index, the increase in accuracy will allow more successful pairing, i.e. the pairing will be more similar to pairing based on true additive genetic values. We did not consider this point as parents in our analysis were not mated assortatively by an index. There is a need to study all effects of index selection in realistic and dynamic scenarios.

Outstanding problems can be studied by simulation. An interesting model is the sequential mate selection rule described by SMITH & HAMMOND (1987). This selection rule can be used in a multiple generation context and it takes full advantage of mixed model methodology. Consequently, we are able to use information on preassorted relatives and we can do this free of mating bias (FERNANDO & GIANOLA, 1984 ; GOFFINET, 1983). Such simulation studies should also consider inbreeding, and other aspects of finite population size, overlapping generations, variable selection intensities between sexes and selection beyond 2 generations.

Assortative mating and more generally mate selection, will be found to be very useful in the quest for additive merit. For example, nucleus breeding schemes have proven useful (JAMES, 1977) and these are a subset of mate selection.

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