

Some basics about mating schemes

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Abstract

In animal breeding after selection of the breeding animals a second step is introduced: the matching of a male and a female. This mating can occur randomly or assortatively. Primary reasons for the application of mating are exploitation of non-additive genetic effects (preference of heterozygote), anticipating on non-linearity of profit functions (profit heterosis, maintain or reach optimum level in progeny, and avoid extremes or specific classes), and the desire to influence genetic (co)variances (reduce variability, increase variance to maintain or increase possibilities for selection, restrain inbreeding, and effects on genetic correlations). This paper gives an overview on definitions and applications and details some theory on the influence of mating on genetic (co)variances.

1. Introduction

The Oxford Dictionary of Current English defines ‘to mate’ as: “come or bring together in marriage or for breeding: fit well (with)”. In animal breeding, this is exactly what occurs when mating animals: fitting a pair of (pre-selected) animals for breeding the next generation. There are many different ways in which mating can occur. The most well known way is probably the random mating. There are two main ways in which random mating can be defined (Jorjani, 1995):

- the (pre-selected) animals are mated without method or conscious choice, and
- the equal chance of mating with any of the opposite sex, measured by phenotypic correlation between mates which should be zero in case of random mating.

Neglecting the fact that it is very likely that all finite populations will have some degree of ‘matched’ (assortative) mating due to accidentally mating of related animals, assortative mating can also be practised on purpose. It is this

type of assortative mating that will be considered in this paper.

There are several reasons for applying non-random mating systems

- exploiting non-additive genetic effects (e.g., heterosis or specific combining ability),
- exploiting or anticipating on non-linear profit functions, and
- influencing population (co)variances.

This paper will briefly summarise definitions and possible applications of mating systems, and will provide some details on the influence of non-random mating systems on genetic (co)variances.

2. Definitions

Mating is ‘making sire-dam combinations’. Mating can be either randomly (RM) or assortatively (AM). When assortatively, the intent can be either to mate similar sires and dams preferentially (**positive assortative mating**, PAM) or non-similar sires and dams preferentially (**negative**

assortative mating, NAM). NAM is often also referred to as dis-assortative mating, corrective mating or compensatory mating.

AM can be based on true (known) genotypes of animals (e.g., gene or marker haplotypes), or on phenotype of the animals. In between these possibilities is the criterion of predicted breeding value. Another type of criterion is the additive genetic relationship between sire and dam, used either to create closely inbred lines or to delay inbreeding and reduce inbreeding trend (e.g., minimum co-ancestry mating).

The degree of assortative mating is measured by the marital correlation, which is the correlation between mates for their (true) breeding values for the mating criteria (Lande, 1977; Gimelfarb, 1981). In case of AM on phenotype, other authors use the phenotypic marital correlation as a measure of the degree of assortative mating; the genetic marital correlation is equal to the product of the phenotypic marital correlation and the accuracy of selection (Crow and Felsenstein, 1968; Baker, 1973).

Apart from the marital correlation, the degree of assortative mating can also be denoted by the fraction of the sires and dams mated assortatively: 0 is fully RM.

A specific form of AM is Mixed Assortative Mating (MAM). MAM can be used in case two separate traits are to be combined in a specific way in the offspring (e.g., mating sires with high performance for growth and dams with high performance for reproductive traits and *vice versa*). MAM changes the genetic correlation between traits over generations; positive MAM (high trait 1 with high trait 2) increases, and negative MAM decreases the genetic correlation (Gianola, 1982; Campo and Turrado, 1997).

Another way of differentiating between mating systems is in hierarchical versus factorial designs. With hierarchical or nested designs, sires

are mated to multiple dams and each dam is only mated to one sire (or vice versa, dams are mated to multiple sires and each sire is only mated to one dam, but this is not readily practised in livestock breeding). With factorial or cross classification designs, sires are mated to multiple dams, and dams are mated to multiple sires. In a complete factorial design, all sires are mated to all dams, and all dams are mated to all sires.

Generally, first a number of sires and dams are selected based on their predicted breeding value. Secondly, selected sires and selected dams are mated. Another option is that first all possible combinations of sires and dams are considered, and (potential) offspring of all combinations are listed, and next, (potential) offspring are selected. In this second option, called 'mate-selection', selection of sires and dams is only an implicit step (Allaire, 1980; Kinghorn, 1987). In both options, selection and mating are in principal independent processes. In practice, however, selection and mating often interfere. A very common example is where sires are pre-selected, and next mating to dams is partially based on non-random, but rather on predicted breeding values, resulting in more dams mated to better sires. In this example, the average predicted breeding value of pre-selected sires will be lower than the weighted (according to frequency of mating) average of the mated sires.

3. Applications

Primary applications of assortative mating systems are in exploiting non-additive genetic effects, anticipating on non-linearity of profit functions, and the desire to influence genetic (co)variances.

Non-additive genetic effects

With the existence of dominance genetic effects, the heterozygous genotype is favoured over the homozygous genotypes (especially in a situation of over-dominance). Systematic crossbreeding, i.e. a mating system combining sires and dams from different lines, can increase the frequency of heterozygous genotypes. Exploiting this genetic heterosis is part of the increased efficiency when using specialised sire and dam lines (Moav, 1966). Systematic crossbreeding can also exploit other non-additive genetic effects, such as epistatic effects, or more general, exploit general or specific combining abilities of lines (Falconer, 1989).

The within-population equivalent of systematic crossbreeding is the selection and directional use of individual animals with high dominance genetic effects (clone line selection; De Boer, 1994) or high within-line specific combining ability. For the same purposes, but addressed from a reverse angle, avoiding homozygous genotypes is practised to avoid inbreeding depression.

In current sire-advising programmes, minimum co-ancestry mating is used not to reduce population inbreeding trend, but primarily to avoid that animals at commercial production farms will have extreme high levels of inbreeding, in order to avoid high inbreeding depression and high frequencies of genetic defects by (deleterious) recessive alleles.

Non-linear profit

Systematic crossbreeding of specialised sire and dam lines as a mating system can be used to anticipate on non-linear, multi-trait profit contours (Moav, 1966). Also within-population, planned mating can increase the mean value of the non-linear profit in the progeny by either

aiming at maintaining or more closely reaching the optimum (population) level in progeny. The advantage of planned mating will be greatest for traits with high heritability and population mean close to the economic optimum (Weller et al., 1996). Apart from this advantage when generally considering continuous, non-linear profit functions, planned mating can be addressed to avoid extremes or specific classes or ranges of phenotypes with discontinuous profit functions. As an example, a commonly practised mating system is the use of a calving ease bull on heifers to avoid dystocia (Meijering, 1986).

Influence genetic (co)variances

A general feature of mating systems is that they can be used to influence variation in the population. A common practice is to use systematic crossbreeding to reduce variability of the product, especially in meat type animals. But likewise mating can be used to reduce variability in animal characteristics, for example at herd level (like reducing variability in milking speed to enhance efficient milking).

Mating systems can be used to increase within-population variance to maintain or increase possibilities for selection and mating in future generations. Mating can also be used to split a population in highly inbred lines to redistribute population variance. Advantages are in selecting specialised sire and dam lines with a uniform genetic background. Also, in theory, with many highly inbred lines, total population variance will increase (Falconer, 1989).

Related to maintaining within-population variance is reducing inbreeding trend. Mating systems (especially minimum-co-ancestry mating) can be used to reduce

inbreeding trends in populations (Caballero *et al.*, 1996), or likewise to increase genetic trend at a predetermined, constrained rate of inbreeding in the population (Sonesson and Meuwissen, 1999). Reducing inbreeding trend refers to reducing a surplus of homozygous genotypes relative to parental, base population allele frequencies (F_{ST}). Also Hardy-Weinberg dis-equilibrium (relative surplus of homozygous genotypes relative to allele frequencies in the current population, F_{IS}) can be avoided by specific mating systems. This is not only practised in livestock breeding, but also natural mating systems to adhere variability are observed (e.g., Wenink *et al.*, 1999).

Breaking or enforcing genetic correlations can be accomplished by mixed assortative mating (MAM, discussed above; see also Tallis and Leppard, 1988).

4. Effects of mating on population variance

The variance among total additive genetic values can be written as the sum of the (co)variances of the n component genes/loci,

$$\sigma_A^2 = \sum_{i=1}^n \sigma_{A_i}^2 + 2 \sum_{i=1}^n \sum_{j=i+1}^n \sigma_{A_i A_j}$$

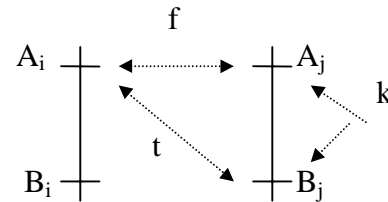
where, i and j are individual genes. The additive genetic variance ($\sigma_{A_i}^2$) at one gene with two alleles is (Falconer, 1989)

$$\sigma_{A_i}^2 = 2p_1 p_2 \alpha^2.$$

with alleles A_1 and A_2 at a certain locus having frequencies p_1 and p_2 , and

allele substitution values $p_2 \alpha$ and $-p_1 \alpha$, respectively.

Let f be the correlation between homologous alleles, k the correlation between non-homologous alleles on the same gamete, and t the correlation between non-homologous alleles on different gametes:



The covariance within a pair of alleles is $p_1 p_2 f \alpha^2$, and there are n pairs. The covariance between homologous alleles on the same (maternal or paternal) gamete is $p_1 p_2 k \alpha^2$ and there are $n(n-1)$ combinations. Likewise, there are $n(n-1)$ pairs of non-homologous alleles on different gametes with covariance $p_1 p_2 t \alpha^2$. Putting all this together (Crow and Felsenstein, 1968; Baker, 1973)

$$\sigma_A^2 = 2n p_1 p_2 \alpha^2 [1 + f + (n-1) k + (n-1) t]$$

In fact, f is a measure of Hardy-Weinberg dis-equilibrium, and k and t are measures of linkage dis-equilibrium. Without further specification, f , k and t are usually assumed to be zero, which means that σ_A^2 reduces to $2n p_1 p_2 \alpha^2$.

Let f^* , k^* and t^* be the correlations in the (selected) parental fractions of the population. Selection induces gametic phase linkage dis-equilibrium (Crow & Felsenstein, 1968; Bulmer, 1971; Baker, 1973). When no recombination occurs, k^* in the progeny (the correlation between alleles on the same gamete) will be equal to k^* in the parental fractions. In case of recombination fraction c ,

$$k' = (1-c)k^* + c t^*.$$

Correlation f^* and t^* will be broken down during gametogenesis. However, with assortative mating, the correlation between gametes joining in offspring depends on the relative magnitude of the marital correlation r between mated sire and dam (Crow and Felsenstein, 1968)

$$f' = t' = r / 2n [1 + f^* + (n-1) k^* + (n-1) t^*].$$

According to the sign of r , mating will result in relatively higher or lower frequencies of homozygous genotypes, and consequently more or less additive genetic variance in the population.

Bulmer (1971) expanded the principle of linkage dis-equilibrium as a result of selection to an infinite-locus model, and derived formula to calculate an equilibrium variance loss: the 'Bulmer effect'. Selected individuals, parents for the next generation, represent one tail of the distribution of the index selected for. As a consequence, the variance on the index in the selected parents must be less than that of the whole population

$$\sigma_A^{2*} = \sigma_A^2 + r_{IH}^2 \gamma \sigma_A^2 = (1 + r_{IH}^2 \gamma) \sigma_A^2$$

where r_{IH}^2 is the accuracy of selection and $\gamma = -i (i - x)$, with i is the selection intensity and x is the corresponding deviation at the point of truncation from the population mean. The additive genetic variance in the following generation is represented by

$$\sigma_{A(t+1)}^2 = \frac{1}{4} \sigma_{AM(t)}^{2*} + \frac{1}{4} \sigma_{AF(t)}^{2*} + \frac{1}{2} \sigma_{A(0)}^2$$

where subscript t denotes the generation number, subscript F an M denote populations of females and

males, and superscript $*$ denotes the selected population. σ_{A0}^2 is the original additive genetic variance in the base population and represents Mendelian Sampling variance. With prolonged selection over generations, the equilibrium reduction in additive genetic variance will be equal to

$$D_{equilibrium} = \sigma_P^2 \cdot [2\gamma_{IH}^2 - 1 + \sqrt{1 - 4\gamma_{IH}^2(1 - r_{IH}^2)}] / 2(1 - \gamma)$$

Following the theory of Bulmer (1971), Tallis & Leppard (1987) expanded this equation to a situation incorporating assortative mating; with assortative mating calculation of γ is changed to γ'' which is

$$\gamma'' = (\gamma_M + \gamma_F) / 2 + r \sqrt{1 + \gamma_M} \sqrt{1 + \gamma_F}$$

where subscript M and F refer to selected male and female parents.

As a general conclusion, the mating system will determine the correlation between alleles in joining gametes, and thereby influence variance components (additive, dominance, epistatic, and their covariances; Jorjani, 1995).

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