A method to accommodate variable male mating success when managing diversity under mixed mating scenarios

B.P. Kinghorn[1,2*] and A.J. Kinghorn[2]

[1]*University of New England, Armidale, Australia;* [2]*MateSel, Australia;* [*]*bkinghor@une.edu.au*

Summary
Under mixed mating scenarios, group-housed males compete directly with each other to mate females. Variation in mating success can be high, and highly skewed, resulting in higher parental coancestry and lower retained diversity than what would be achieved under equal contributions, or Poisson-distributed contributions. This paper presents a method to predict the distribution of mating success and its effect on parental coancestry, together with a fast method to calculate increased parental coancestry for application in optimal contributions selection.

Introduction
Under multi-sire mating and other mixed mating scenarios, multiple males and females are located in the same facility, and males can freely compete with each other to mate females. Competition between males leads to a skewed distribution of male contributions, giving an increase in mean parental coancestry (**PC**) and a reduction in genetic diversity. This paper presents a method to predict this increase in PC, and to account for this under optimal contributions selection (**OCS**). The underlying model uses order statistics to help predict the proportion of matings achieved by each male ranked in order of mating success.
For practical application it is computationally slow to recalculate PC in the standard manner when accounting for this increased variation in male contributions. A fast method is presented whereby only the predicted increase in PC due to variable male mating success is calculated, as a function of fitting the model presented.

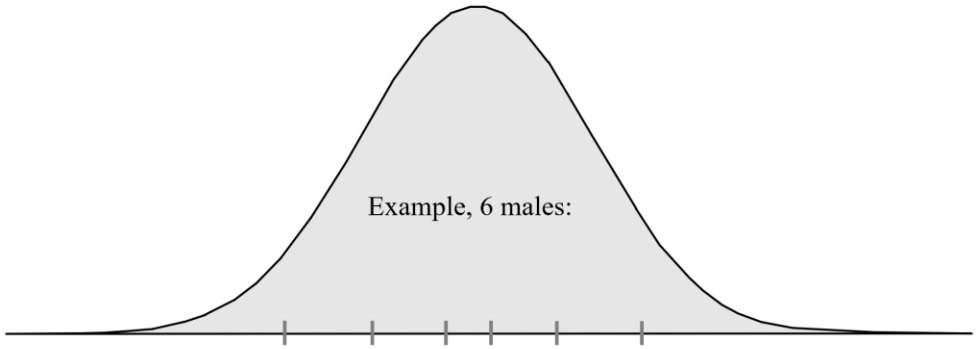
Materials & Methods
Predicting sire mating success proportions. For this, we used the function described by Kinghorn (2023), which predicts the proportion of matings achieved by the j^{th} most successful sire out of a pool of n sires as:

$$\frac{(S_j - S_n + m)^p}{\sum_k (S_k - S_n + m)^p} \quad where \quad S_j = j * i_{j,n} - \sum_{k=1}^{j-1} k * i_{k,n} \qquad (1)$$

Here, $i_{j,n}$ denotes the selection intensity of selecting j out of n individuals. The parameters m and p are calibration constants controlling the variability of mating success and the skewness of mating success. A conceptual description of how Eq. 1 operates is shown in Fig. 1.

Data analysis to parameterise the model. We used five datasets from sheep, beef cattle and fish, where males had been used in mixed mating groups, and the parentage of resulting progeny had been assessed for each male parent using genomic information on parents and progeny. Males were ranked on mating success, and Eq. 1 was used to predict the percentage of matings that males would achieve when ranked highest to lowest on mating success, as in the last line of Fig. 1.

The fit was made by minimising the sum of squared errors between predicted and realised mating success of ranked males, by varying parameters *m* and *p* in Eq. 1. As seen in Fig. 2, making this fit across datasets gave good results, leading to setting default parameters of *m*=2 and *p*=3.5 (Kinghorn, 2023).



From Selection intensities:	-1.26	-0.66	-.21	.21	.66	1.26
Set lowest to *m* = 2:	2	2.6	3.0	3.5	3.9	4.5
Set to Power *p* = 3.5:	11	29	49	77	119	197
Scale to percentage:	2.3	6.0	10.2	15.9	24.7	40.9

Figure 1. Example calculation of percentage mating success of six males in a mixed mating group, using Eq. 1 with *m*=2 and *p*=3.5.

Calculating modified Parental Coancestry. Unequal contributions from the males within a mixed mating group (MMG) results in an increased sum of squares of genetic contributions of males in the group, compared to the equal contributions that we might achieve under fully controlled matings. For simple presentation we will first consider *twice* the PC which is simply **x'Ax**, where **x** is a vector of contributions and **A** is the NRM or GRM. The increase in twice PC that is caused by unequal contributions from the males in MMG *k* is:

$$\sum_{i}^{n_k}\sum_{j}^{n_k} x_i A_{i,j} x_j - \sum_{i}^{n_k}\sum_{j}^{n_k} \bar{x} A_{i,j} \bar{x} = \sum_{i}^{n_k}\sum_{j}^{n_k} \left(x_i x_j - \bar{x}^2\right) A_{i,j} \quad (2)$$

where n_k is the number of males in MMG *k*, x_i is the contribution of ranked male *i* to the currently selected population (as derived from the result of Eq. 1) and $\bar{x}$ is the mean contribution of males in the group. This can be broken down to diagonal and off-diagonal components:

$$\sum_{i}^{n_k} (x_i x_i - \bar{x}^2) \bar{A}^{diag} \quad (3)$$

$$\sum_{i}^{n_k}\sum_{j\neq i}^{n_k} \left(x_i x_j - \bar{x}^2\right) \bar{A}^{off-diag} \quad (4)$$

Notice that we use mean relationships on the diagonal and off diagonal: Just as we cannot modify predicted mean parental EBV because we cannot predict which individual males will make greater contributions, we cannot know which individual males will contribute more to PC. However, we can predict the impact of unequal use on PC.

Given that:

$$\sum_{i}^{n_k}\sum_{j\neq i}^{n_k} x_i x_j = n_k^2\,\bar{x}^2 - \sum_{i}^{n_k} x_i^2 \quad \text{and} \quad \sum_{i}^{n_k}\sum_{j\neq i}^{n_k} -\bar{x}^2 = -n_k(n_k-1)\,\bar{x}^2 \quad \text{then}$$

$$(4) = \left((n_k^2 - n_k^2 + n_k)\bar{x}^2 - \sum_i^{n_k} x_i^2 \right) \bar{A}^{off-diag} = -1. \left(\sum_i^{n_k} (x_i^2 - \bar{x}^2) \right) \bar{A}^{off-diag}$$

The resulting increase in population PC, over all MMG groups is thus given by adding (3) and (4), summing over MMG (which gives difference in meaning of subscripts, as described below) and dividing by 2 to match PC=**x'Ax**/2:

$$\sum_k^{MMGroups} \left(\sum_{ji}^{n_k} (x_{k,i}^2 - \bar{x}_k^2)(\bar{A}_k^{diag} - \bar{A}_k^{off-diag}) \right) \Big/ 2 \qquad (5)$$

where *MMGroups* is the number of mixed mating groups, $x_{k,i}$ is the contribution from the i^{th} male in the k^{th} MMG, $\bar{x}_k$ is the average contribution of males in the k^{th} group (the contribution each would make under equal contributions), $\bar{A}_k^{diag}$ is the average of the diagonals in the NRM or GRM among males in the k^{th} group, and likewise for the off-diagonals for $\bar{A}_k^{off-diag}$.
Eq. 5 is generally fast to compute as we only need to handle selected males within each MMG, and almost no computational time is added when running a typical OCS application.

Results

The model for predicting percentage mating success for ranked males was fitted using data sets from beef, sheep and fish, where the realised mating success of each male had been recorded, using parent and progeny genotype data. A single parameterisation of the model worked remarkably well across species and numbers of males in each MMG (Fig. 2).

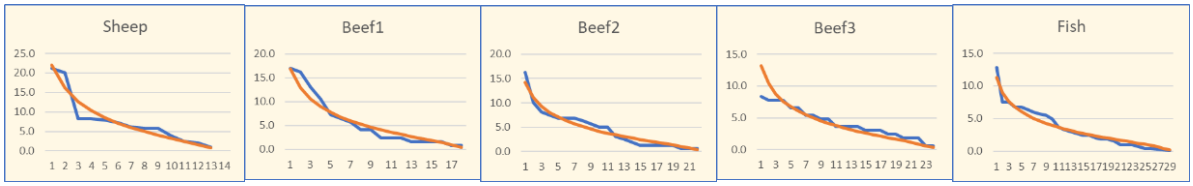


Figure 2. Realised data (blue lines) and predictions from the current model (red lines) for mating success (vertical axis) of males ranked high to low (horizontal axis). For the dataset Beef3, the first four ranked males all had similar success, but in all other cases predictions were close. A single parameterisation of the model (m=2, p=3.5 in Eq. 1) was used for all datasets.

The numbers of males in the five datasets analysed were (13, 18, 22, 24 and 29); the correlation between predicted and actual numbers of matings per sire, ranked on number of matings realised, averaged 0.967 (range 0.952 to 0.980); and the ratio of s.d. of predicted matings to s.d. of realised matings averaged 1.006 (range 0.839 to 1.396).

An example of adding this value to PC that has been calculated assuming equal male contributions is shown in Fig. 3.

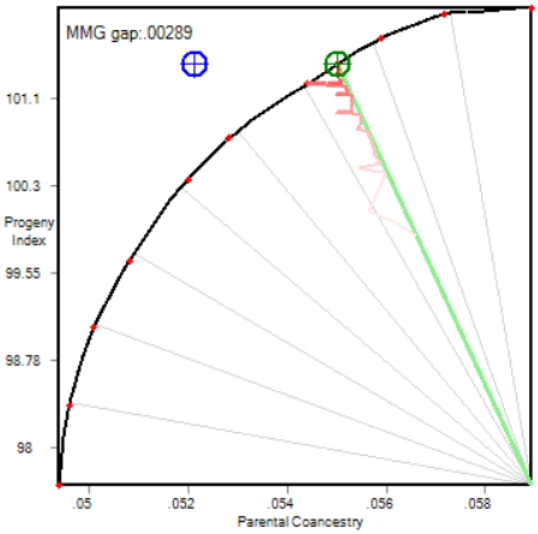


Figure 3. Example impact of accounting for variable male mating success in an OCS example using mixed mating groups. For the current solution, the blue icon shows PC under assumption of equal mating success for males within each of the 4 MMG groups involved. MMG gap is the current value from Eq. 5, and the green icon shows the corrected solution with a higher PC. In this case, optimisation is based on corrected PC, and the pareto front goes through the green icon.

Discussion

The allocation of males and females to mixed mating groups uses the increased PC in the overall objective function, thus removing the optimistic assumption that competing males make equal contributions. One impact is to encourage use of related males within groups (closing the MMG gap in Fig. 3). If all males in a group are clones of each other, variable mating success is not a problem. However, selecting highly related males into groups will increase overall PC (shifting both blue and green icons to the right in Fig. 3), and so the optimisation will balance these competing components. This is done by simply using overall corrected PC in the objective function, with the pareto front passing through the green icon in Fig. 3.

Variable male mating success is probably not important at all wherever male contributions will eventually be controlled at actual mating time. This happens when 'mixed mating groups' are formed in order to assemble matched male and female cohorts, usually for migration among breeding units such as nucleus farms, test stations, AI stations and multiplier farms. If this eventually leads to individual-animal mating decisions, variable male mating success is not an issue. In such cases, the option is chosen to pass the pareto front through the blue icon in Fig. 3.

Conclusions

The method to predict distribution of male mating success made a good fit across all datasets tested with the same parameterisation used for each of these. This is promising for application quite widely, although practitioners should use their own data for parameterisation wherever possible. Computational speed for parental coancestry is only slightly slower compared to individual sire mate allocations. Application of these methods has progressed across several breeding industries.

Acknowledgements

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References

Kinghorn, B.P. (2023) Managing unequal male reproductive success. https://youtu.be/GkqGDFZPUF4