

MANAGEMENT OF INBREEDING AND COANCESTRY TO TARGET SHORT-TERM AND LONG-TERM GENETIC GAINS

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SUMMARY

Inbreeding is not heritable. This means that breeding for low inbreeding generally has a transient and non-accumulating impact over generations. This is a bit like selecting for a trait that has a heritability of zero. However, coancestry (taken as the mean coancestry between an individual and the rest of the selected population) is heritable. Breeding for low coancestry in any one generation has a lasting impact over generations to increase genetic diversity and decrease the population mean inbreeding level. These issues have been poorly understood in some industries. Appropriate management of both coancestry and inbreeding is required to optimise the balance between short-term and long-term genetic gains, as well as to maintain genetic diversity. This paper tests and illustrates the implementation of such strategies. Management of coancestry is critical, whereas management of progeny inbreeding is of some transient value.

INTRODUCTION

A high rate of genetic gain for the desired breeding objective(s) is central to most breeding programs. However, to sustain a high rate of gain in the long term, genetic diversity has to be maintained. Without genetic diversity, the better individuals are no better genetically than the worse individuals, and genetic gain stops.

Genetic diversity reduces more quickly in smaller breeding populations: In any one generation, few individuals contribute to the genetic mix in the long-term. Moreover, their contributions become less evenly distributed, giving more loss of diversity. This is because few parents in each future generation means that some individuals' descendant lineages die out, just by random chance. Selection on an index accelerates this loss of diversity, as less meritorious lineages die out more quickly than by chance.

This loss of diversity is essentially the same as the increase in the level of inbreeding. With a small population size, it becomes inevitable that relatives are mated with each other, and their progeny are thus inbred.

The inbreeding coefficient of an individual is the probability that the two genes that it inherits from its two parents are identical by descent – they are exact copies of a gene carried by an ancestor that is in the pedigree of both of its parents. However, an individual cannot pass its merit for inbreeding to its progeny – for that to happen we would have to squeeze two genes into one sperm or egg, and that is not how it works. Inbreeding is not heritable.

Highly inbred individuals have more identical genes, and thus have less genetic diversity or variation *within themselves*, and this is a key reason that they tend to survive and perform poorly. However, within a small closed breeding population, there is also generally less genetic variation *among* individuals, because they share so many recent ancestors in common. The reduction in genetic diversity is simply related to the increase in average inbreeding coefficient:

Genetic variation = (1 – average inbreeding coefficient) x *genetic variation without inbreeding*.

So, inbreeding in a small closed population leads directly to loss of genetic diversity. We can reduce the rate of increase in inbreeding in three related ways:

1. Use more individuals as parents
2. Select individuals that are on average less related to each other across the group
3. Allocate more matings to individuals that are less related to the rest of the population

All of these are accommodated in correct balance with each other when we select parents and the numbers of matings to allocate to each by minimising **the mean Parental Coancestry (PC)** of the selected group. The coancestry between two individuals is the same as the inbreeding coefficient of the progeny they would produce. This means that Parental Coancestry would be the expected mean inbreeding in progeny if we had random mate allocation, including self-mating at random! We cannot achieve this in most species, so Parental Coancestry is in fact a measure of contribution to inbreeding in later generations – **if we keep Parental Coancestry low, we keep long-term inbreeding low**. When combined with consideration of genetic gain, this constitutes Optimal Contributions Selection, whether coancestry and inbreeding are derived from pedigree or genomic information (Meuwissen *et.al.* 2021).

The three points above all relate to selection of individuals to be used as parents, with no attention to mate allocations. So, in addition, we can delay the expression of inbreeding by avoiding the mating of relatives, reducing inbreeding in the next generation. However, this only delays the inevitable mating of relatives in later generations. So, **if we avoid the mating of relatives, we keep short-term inbreeding low**. This paper examines the interplay of these two inbreeding management strategies, together with the degree of emphasis on genetic gains.

MATERIALS AND METHODS

A small population was simulated using PopSim (<https://www.youtube.com/watch?v=5K4Q7SkBdMk&t>) with the following properties: Discrete generations for simplicity, 25 breeding females each producing 4 offspring of random sex, maximum 10 females mated per male, BLUP selection on a single trait with heritability 25%.

Parental Coancestry was targeted to increase over $t = 20$ generations at the same closely-controlled set of rates across treatments for Progeny Inbreeding. The rates chosen were dictated using different values for the balance between genetic merit (“Progeny Index”) and Parental Coancestry, these being 0, 25, 45 and 75 Target Degrees (TD), where 0 degrees puts full emphasis on high Progeny Index, and 90 degrees puts full emphasis on low Parental Coancestry (Figure 1; and Kinghorn and Kinghorn, 2021).

However, policies on avoiding Progeny Inbreeding (and many other factors) can affect outcomes for Parental Coancestry. For example, strong emphasis on decreasing Progeny Inbreeding can result in decreased Progeny Index and increased Parental Coancestry in any one generation, as seen for the current solution in the Figure 1.

So rather than using TD, a hard limit was placed on maximum permissible Parental Coancestry, increasing each generation. This was done by first generating simulated populations at each of the three TDs > 0 (as 0 TD is unconstrained for Parental Coancestry), and the realised values for Parental Coancestry in each generation were then used to set a target maximum Parental Coancestry each generation in subsequent simulations. This approach was needed to give comparable results across treatments.

For each TD, three weightings for avoiding Progeny Inbreeding were applied ($W = 0, -1, -100$; See Kinghorn and Kinghorn 2021), plus a fourth treatment for which only close matings (full sibs, half sibs, parent-offspring) were avoided. All results are the means for 20 replicate simulations.

RESULTS AND DISCUSSION

Figure 2 shows a wide range of results for Progeny Inbreeding and Progeny Index across TDs

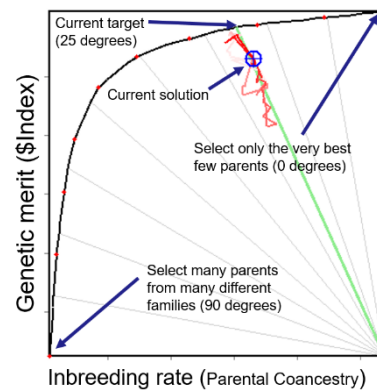


Figure 1. Balancing Genetic merit and Genetic diversity using Target Degrees

and treatments for Progeny Inbreeding (F). It can be seen that a strong weighting against inbred progeny ($W=100$) strongly reduces F, especially at low TDs. However, the need to select individuals able to give this outcome results in much lower Index response. For all TDs, the best strategy for genetic gain is a moderate weighting ($W=1$) against Progeny Inbreeding.

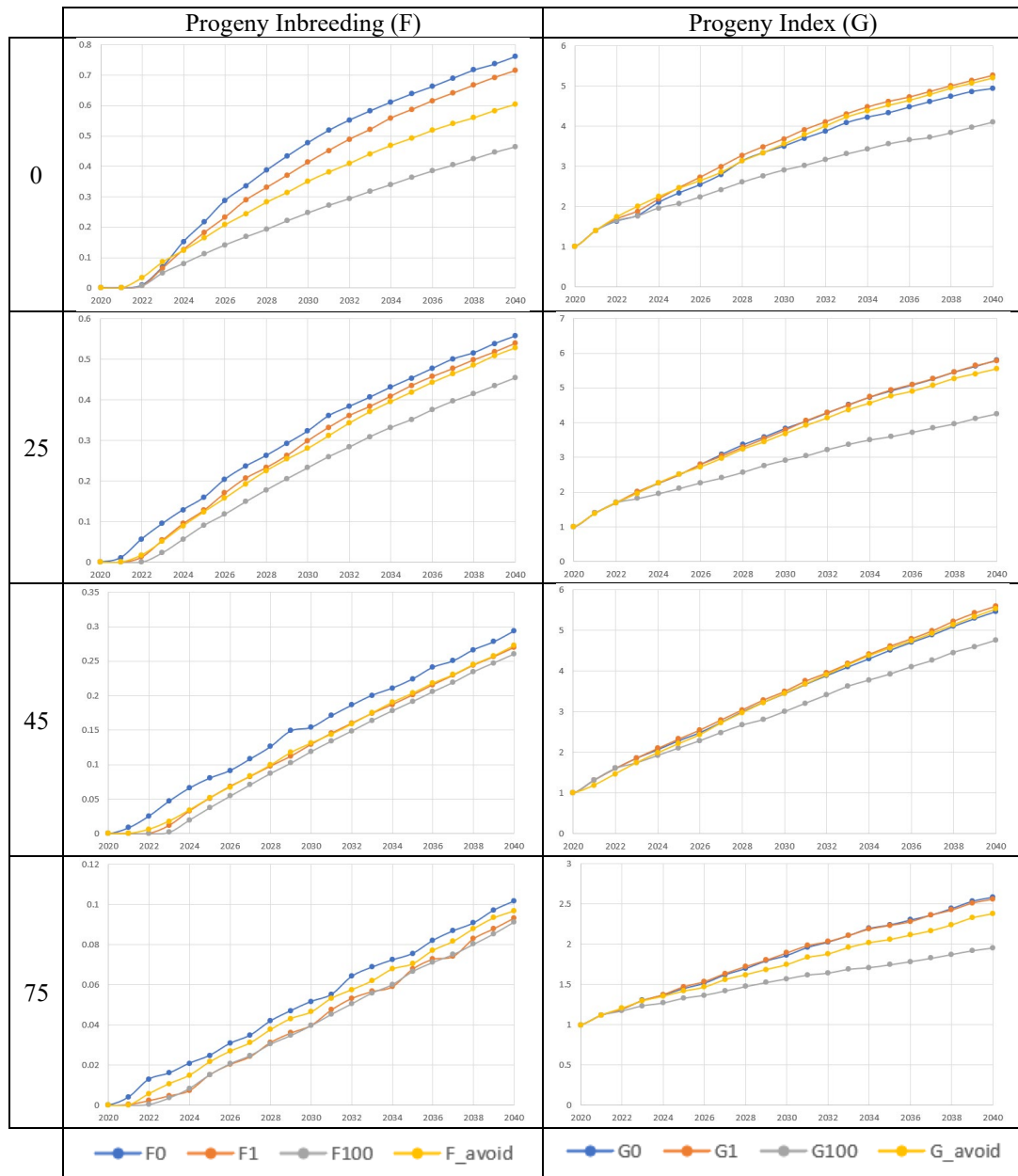


Figure 2. Mean Progeny Inbreeding and Index by year for TargetDegrees ranging from 0 (aggressive) to 75 (conservative). Treatments are weightings of $W = 0, 1,$ and 100 against Progeny Inbreeding, plus avoidance of mating close relatives, “avoid”.

The “avoid” strategy gives substantially reduced Parental Coancestry (Figure 2). Detailed observation shows that this is because avoiding the mating of close relatives has usually required selection of individuals that would not otherwise be selected. This causes increased diversity (reduced Parental Coancestry), but it also decreases selection response. However, this is due to the very small population size used here. In most breeding programs, use of this strategy will lead to re-shuffling of matings to avoid mating close relatives with little or no effect on selections.

Does the reduced inbreeding under $W>0$ mean we are increasing genetic diversity? Not at all! Mean Parental Coancestry is the measure of diversity, and this is essentially identical for $W=0$ and $W=1$ in Figure 3. Progeny Inbreeding for $W=0$ lags behind Parental Coancestry as follows: one generation, because the inbreeding in an animal equals the coancestry between its parents, plus about one more generation in this case, because calculation of Parental Coancestry includes self relationships, as indicated previously. It is this latter bit that accommodates the very real impact of small population size on long-term inbreeding. Progeny Inbreeding is usefully reduced by using $W=1$ in figure 3, with no cost to coancestry or genetic gain. In fact there may be some positive effect on gain due to reduced inbreeding depression.

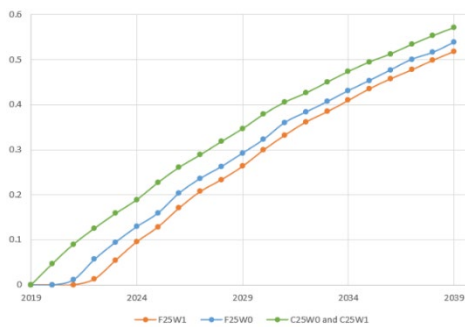


Figure 3. Parental Coancestry and Progeny Inbreeding trends for $W=0$ and $W=1$ under $TD=25$

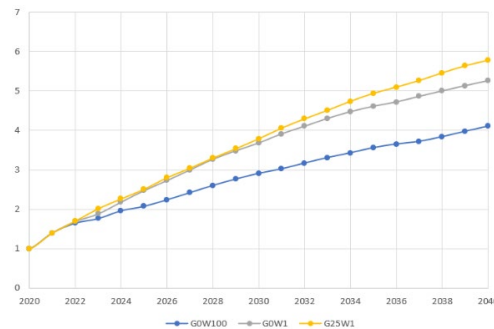


Figure 4. Genetic gains for strategies to decrease progeny inbreeding, coancestry, and both

As a “bottom line”, Figure 4 shows that breeding to strongly reduce progeny inbreeding ($TD=0$, $W=100$) results in poor selection response. Moderate pressure to reduce progeny inbreeding ($TD=0$, $W=1$) is much better, but long-term response is reduced because of lack of attention to Parental Coancestry. The best strategy here is moderate attention to both Parental Coancestry and Progeny Inbreeding ($TD=25$, $W=1$). This strategy gave 12.2% more response in Index, and leaves the population with 61.5% more genetic variation after 20 generations. Overall, for genetic gain, coancestry management was 4.9 times more valuable than inbreeding management, and it was 7.7 times more valuable for genetic diversity.

CONCLUSIONS

To manage inbreeding and genetic gain in breeding populations, attention to keep Parental Coancestry low (eg. choosing and invoking an appropriate Target Degrees) is generally very much more important than steps to reduce Progeny Inbreeding. However, both play a role and both should be attended to appropriately.

REFERENCES

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 Meuwissen T.H.E., Sonesson A.K., Gebregiwergis G. and Woolliams J.A. (2020). *Front. Genet.*. <https://www.frontiersin.org/article/10.3389/fgene.2020.00880>