Breeding the best with the best will always give you the best – right?

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Summary

- Breeding the best to the best does not always give you the best!
- Large variability in genetic merit exists, even among full-sib progeny, and genomics can help identify the superior (and inferior) animals earlier
- Reliability is a measure of how closely the published proof of an animal is likely to reflect its true genetic merit; the lower the reliability, the greater the likelihood that the animal's proof may change over time but there is an equal probability of the proof increasing as there is decreasing
- When choosing whether to use a high reliability bull of inferior index value or a lower reliability bull but with superior index value, both the differential in index values of the bulls and the difference in reliability should be considered
- Published ICBF genetic evaluations are the most accurate way to identify the most suitable animal, male or female

Introduction

Breeding the best with the best will always give you the best – right? Wrong! Breeding the best (for a trait) with the best (for that trait) increases the chance of producing a good animal. Firstly it only increases your chances, and secondly the assumption only holds valid for that trait; the latter is predicted on no other limiting factor hindering the expression of the genetic superiority in that trait. For example, continuously breeding for greater live-weight gain may not always yield a return, as was the case in broilers because of the unfavourable correlated response in animal welfare (e.g., bone strength, sudden death syndrome). If breeding was so easy then everyone would have animals excelling in all traits – breeding is as much about luck as it is about science and lineages. Science and tracing of pedigree lines merely serve to reduce the reliance on luck. In this paper I would like to explain the science behind why breeding the best with the best won't always give you something better but also what the science of breeding can do to increase the chances of genetic gain in the population. As a country we are interested in increasing the genetic potential of the entire population and the justification of schemes like the beef data and genomics programme is not that every female excels, but instead, the entire population of females are genetically superior to the immediately preceding generation.

What the hell is heritability and why should we get hung up about it?

Heritability can be interpreted two different (yet related) ways:

- How much of the variability observed in a field of similarly managed animals is due to differences in genes that are directly transmitted from one generation to the next.
- 2. What is the correlation between the variability in performance that you observe in the field versus the actual genetic makeup of the animal.

Heritability does not mean how much of the performance of an animal is inherited from its parents. For example, if the heritability of growth rate is 0.40 (i.e., 40%), this does not mean that 40% of the growth rate of an individual is inherited from its parent. Table 1 summarises the heritability estimates for a range of different traits in beef cattle. Traits associated with functionality (e.g., health, fertility) tend to be lowly heritable, while traits associated with morphology (e.g., size, carcass characteristics) tend to be highly heritable. This is a common generalisation across all species. Despite what is often thought, low heritability, however, does not mean that breeding for improvement will be slow or that a breeding program for low heritability traits will be worthless; similarly, but on the contrary, it was often thought that you can rapidly change high heritability trait. The number of legs a cow is born with is highly heritable – we cannot, however, easily change the number of legs a cow is born with because there is little variability.

Heritability impacts reliability, in that for the same number of progeny records, the reliability will be lower for low heritability traits. This is why for some bulls they may be high reliability for some traits (usually the output performance traits) but lowly reliable for other traits like fertility and survival. The effect in this example is compounded by the fact that slaughter data exists for both male and female progeny at a relatively young age while reproduction data is only expressed by females and

the bull is considerably older when his daughters eventually calve. Nonetheless, it is possible to still achieve high reliability for low heritability traits, it is just more difficult. Therefore, it is possible to achieve as fast genetic gain for fertility as was achieved for growth rate. Hence, the relevance of heritability for breeders and farmers is small.

| Trait | Heritability |
|---|--------------|
| Calving performance traits Direct calving difficulty | 0.10 |
| Maternal calving difficulty | 0.04 |
| Gestation length | 0.35 |
| Calf mortality | 0.02 |
| Performance traits | |
| Carcass weight, conformation & | 0.30 to |
| fat | 0.40 |
| Average daily gain | 0.31 |
| Live weight | 0.39 |
| Efficionev traite | |
| Feed efficiency | 0.33 |
| | |
| Reproduction traits | |
| Calving interval | 0.02 |
| Survival | 0.02 |
| Calving to first service interval | 0.05 |
| Pregnancy rate | 0.02 |
| Health traits | |
| Mastitis | 0.02 |
| Cystic ovaries | 0.03 |
| Lameness | 0.02 |
| | |
| Other traits | |
| Body condition score | 0.20 |
| Docility | 0.20 |

 Table 1. Example of heritability estimates for a selection of traits in beef cattle

How can a calf have a low reliability when his father (and mother) is well proven excellent performers?

The reliability of an animal, based solely on pedigree information, is one quarter the reliability of the sire plus one quarter the reliability of the dam. Therefore, if the sire is 99% reliable, and the dam 30% reliable, the reliability of their newborn calf is only 32%. This is the same worldwide and for all species. The reason is that the sire only

contributes a quarter of the genetic variability to his progeny, the dam contributes another quarter, and the remaining half of the variability is attributable to the sampling of genes from both the sire and dam.

Based on the population characteristics of the replacement index in Ireland, 66% of the sperm in a bull ejaculate will have a replacement index merit within $\pm \in 34$ of each other. This means that half the remaining 33% of the sperm in an ejaculate, if it eventually fertilised an egg, will contribute a replacement index value to the calf of more than $\in 34$ superior to the bull itself. Of course half the remaining 33% of the sperm in an ejaculate, if it eventually fertilised an egg, will contribute a replacement index value to the calf of more than $\in 34$ superior to the bull itself. Of course half the remaining 33% of the sperm in an ejaculate, if it eventually fertilised an egg, will contribute a replacement index value to the calf of more than $\in 34$ inferior to the bull itself. This phenomenon is true no matter if the bull is high reliability or a young stock bull – reliability is irrelevant.

Suppose a bull has an estimated replacement index of $\in 180$ with 99% reliability. The average sperm from an ejaculate is expected to also have a replacement index value of $\in 180$, although the actual replacement index value of 66% of the sperm will lie somewhere between \$146 and \$214; 33% of the sperm will be outside these boundaries. Therefore, there is massive variability in the replacement index value among the hundreds of straws generated from a single ejaculate of an AI bull. There is no way of knowing which is the good straw and which is the bad – at the end of the day it's all luck. The same is true for stock bulls. Reliability doesn't impact this but if you have a high genetic merit bull and if you are unlucky and the poor sperm cell fertilised the cow then the expected genetic merit of the calf could still be better than if you used a poor genetic merit bull but were lucky and the good sperm cell fertilised the cow. Therefore, using a higher index bull increases your chance of having higher index calves but certainly does not guarantee every calf will be high index.

Take the example of human height. Human height is 80% genetically determined. After accounting for differences in gender and ethnicity, the height of 66% of humans lie within 7 cm of the global population mean. Our hunch may be that the variability in height within a family (from the same parents) would be considerably less than what we see among the billions of people worldwide, especially because human height is so strongly influenced by genes and you receive your genes only from your parents. In fact, this is not the case with the 66% of humans from the same parents lying

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within 5.4 cm of their average (although their average may deviate considerably from the global mean). In other words, the variability within a full sib family is 77% of that observed in the entire population. If the heritability of human height was in fact just 10%, then the variability within a full sib family is 97% of that observed in the entire population or in other words almost the same. In summary, the variability in the progeny from the same bull and even the same bull-dam combination is huge and cannot be accurately predicted in advance. Breeding the best with the best does not always give you a better animal – although it does increase your chances.

How can I have (non-identical) twin calves and one is a five star and the other is a one star?

The answer to this question is based on the theory of inheritance just described. Although everyone gets half their genes from their father and half from their mother, each half is actually a relatively random half; in fact two full sibs could genetically be completely unrelated! Non-identical twins occur when the dam has a multiple ovulation and thus is essentially very similar to two calves from the same sire-dam born over consecutive years (sharing a common uterine and post-natal environment, as would be the case in twins, does however affect performance). If the threshold in replacement index determining a one-star is <€43 and the threshold determining a five-star is >€96, then a calf born with a replacement index of €70 and reliability of 30% has a 10% probability of being a one-star animal when genotyped and a 11% chance of being a five-star when genotyped. When the animal is eventually proven (i.e., 99% reliability), there is a 25% probability of the animal being a one-star animal and a 26% chance of being a five-star. For twins, both with a €70 replacement index at 30% reliability, there is a 2% chance that one will be a one-star and the other will be a five-star once genotyped. There is, however, an 8% chance that one will be a five-star and the other will be a two-star or worse once genotyped. Therefore, genetic merit can differ substantially even among non-identical twins or calves born from the same sire-dam combination.

What is all this genomics stuff doing to improve my chances of breeding better stock?

All you know about a new born calf is its sire and dam. The replacement index value of that calf is simply half the sire plus half the dam; the same is true for the terminal index of the calf being simply half the sire plus half the dam. We know, however, from the previous examples described, that animals, although each inheriting half their DNA from their sire and half from their dam, the actual DNA inherited is relatively random and this contributes to the large variability in the progeny. Breeders use visual assessment, and do a good job at it, to assess the expected performance of the animal for growth traits. However, it is very difficult to visually assess for feed efficiency, fertility, survival and many health traits. Even the observed correlations between live animal linear assessments (by trained professionals) and carcass data indicate considerable scope for improving the prediction of genetic merit through access to the real data, as opposed to visual assessments. To achieve this, and achieve high accuracy, one must wait for the sire to have many progeny who in turn express the trait of interest. As previously alluded to, this can take a considerable amount of time for the collection of female traits in daughters.

We know, however, that DNA influences performance, and we know the DNA of an animal is the same throughout its life. Therefore, if we can measure the DNA of a calf at birth, it should provide us with additional information to predict the expected performance of, not only the animal itself, but also its descendants. Although the latter is achieved with lesser accuracy because it is unknown which DNA segments the sire will transmit to its progeny. This is the fundamentals underpinning genomic selection in cattle. However, because each individual has 3 billion pieces of information, it is currently not possible to know the effect of each piece of DNA on each performance trait and thus 100% accuracy is not achievable. As the number of animals with DNA information and performance information increases, the accuracy of genomic evaluations will improve.

What exactly is a good dam line and is it accounted for in genetic evaluations?

DNA is located in two components of cells – the nucleus and the cytoplasm. The DNA which resides within the nucleus, termed the nuclear DNA, constitutes the vast majority of the total DNA and is what is generally only considered in genetic

evaluations. The nuclear DNA is equally transmitted from each parent to the offspring. DNA in the cytoplasm, however, is only transmitted via the ovum and thus only from the dam. No cytoplasmic DNA is present in the sperm. Cytoplasmic DNA does not often mutate, allowing dam linages to be relatively easily traced back many generations. It is this cytoplasmic DNA which is the source of dam linages. However, extensive research in cattle, including from Ireland, clearly show that the contribution of such cytoplasmic DNA to performance traits is generally negligible. Females that in turn, on average have good performing females (would just as easily have good performing males if they also expressed the traits), do so through superior nuclear DNA which is accounted for in genetic evaluations. Dam linages in the strictest sense are not considered in genetic evaluations.

Which bull should I chose – a high index bull with low reliability or a lower index bull with high reliability?

As a purist geneticist, the answer is simple – the higher index bull, since the estimate of genetic merit of each bull is the most accurate estimate. At a practical level, the answer depends on how risk-averse the farmer is. A risk-averse farmer (or any investor) prefers a lower return on investment with known risk (e.g., the lower index bull with higher reliability) than a higher return on investment with more risk (i.e., higher index bull with lower reliability). The decision on which bull to choose is a function of both 1) the difference in index value between the two bulls compared, and 2) the difference in reliability of the two bulls. An example of such a scenario is in Figure 1 for a bull with a terminal index of \in 70 and reliability of 90% versus a bull with a terminal index of either 50%, 70% or 80%.



Figure 1. Probability distribution of the true terminal index of a 90% reliable bull with a terminal index of \in 70 (continuous grey line) versus the probability of the true terminal index of a bull of either 50% reliability (continuous dark line), 70% reliability (long-broken dark line) or 80% reliability (dotted black line) all with a terminal index value of \in 100.

Clearly the higher the reliability the less the bull is likely to move as it accumulates more progeny. Also, what is clear from Figure 1 is that the probability distribution of the lower index bull sometimes overlaps with the probability distribution of the higher index bull; this means that there are times when the true index value of the bull with the lower published index is actually superior to the true index value of the lower reliability bull but with the higher published index value. Table 2 illustrates the same point in tabular form if comparing a 90% reliability bull against a lower reliability bull but with a differing extent of the difference in terminal index between the two bulls. Take for example two bulls differing in terminal index value of €5 but the lower terminal index value bull being 90% reliable, and the higher index value bull being 50% (i.e., upper left cell of Table 2). Then there is a 39% chance that in fact the lower index bull is truly better than the higher index bull. If the difference in terminal index was €30 instead, then there is only a 4% chance that the lower index bull is truly better than the higher index bull. In the first case, the farmer may choose to use the lower index bull but in the second case it would definitely make sense to use the higher index bull. The same calculations but for the replacement index is presented in Table 3. If the choice is between a bull of 90% reliability with a published replacement index of \in 170 and a bull with a reliability of 50% but a published replacement index of \in 200 (i.e., a difference of \in 30) then there is only a 21% chance the first bull is truly better than the second bull.

Table 2. Probability that the true terminal index of a less reliable bull (varying in reliability from 50% to 90%) is less than the true replacement of a 90% reliability bull when the difference in replacement index between the two bulls varies from \in 5 to \in 30.

| | Reliability of less reliable bull | | | | |
|------------------------|-----------------------------------|-----|-----|-----|------|
| Difference in terminal | | | , | | |
| index | 0.5 | 0.6 | 0.7 | 0.8 | 0.9 |
| 5 | 39% | 38% | 36% | 34% | 31% |
| 10 | 28% | 26% | 24% | 21% | 16% |
| 15 | 19% | 17% | 15% | 11% | 7% |
| 20 | 13% | 10% | 8% | 5% | 2% |
| 25 | 8% | 6% | 4% | 2% | 1% |
| 30 | 4% | 3% | 2% | 1% | 0.1% |

Table 3. Probability that the true replacement index of a less reliable bull (varying in reliability from 50% to 90%) is less than the true replacement of a 90% reliability bull when the difference in replacement index between the two bulls varies from \leq 10 to \leq 60.

| | Reliability of less reliable bull | | | | | |
|------------------------------|-----------------------------------|-----|-----|-----|------|--|
| Difference in replacement | 0.5 | 0.6 | 0.7 | 0.8 | 0.0 | |
| INCO | 0.5 | 0.0 | 0.1 | 0.0 | 0.3 | |
| 10 | 39% | 38% | 37% | 35% | 32% | |
| 20 | 30% | 28% | 25% | 22% | 18% | |
| 30 | 21% | 19% | 16% | 13% | 8% | |
| 40 | 14% | 12% | 9% | 6% | 3% | |
| 50 | 9% | 7% | 5% | 3% | 1% | |
| 60 | 5% | 4% | 2% | 1% | 0.3% | |

Conclusions

There is no way to accurately predict the performance of a progeny from a mating – fact! Genetic evaluations use ancestry information to achieve an initial estimate with an associated level of confidence, reflected by the published reliability value. As the animal accumulates information on itself, either through DNA or performance recording, then the reliability increases and sometimes also the proof of the animal will change. Similarly if performance data becomes available on the animal's siblings or cousins this will affect the proof of the animal's parents and in turn the proof of the animal will change even though it itself accumulated no new data.