LIVESTOCK BREEDING, WHERE HAVE WE BEEN AND WHAT LIES AHEAD?

S.P. Miller

Animal Genetics Breeding Unit[*], University of New England, Armidale, NSW, 2350, Australia

SUMMARY

Presented is an overview of recent advancements in livestock breeding, focussing post the implementation of genetic evaluation, which overlaps with the career of the single author. The rise of genomics is presented as a major turning point and the increased gains and future challenges with this technology is presented. Some history of the corporatisation of breeding programs is presented and parallels with the invention of an enabling technology, such as artificial insemination, is illustrated. It is suggested that further advancements in genetic engineering, such as surrogate sires, or the joining of embryonic stem cells to enable 'speed breeding', would be the next turning point. These technologies would create the environment for large corporate investment in sheep and beef cattle and could change the structure of those genetic industries forever.

EARLY FOUNDATIONS

Livestock breeding has changed considerably over time. A century ago selection was based primarily on phenotype and the 'eye' of the breeder played a major role. Compared to selection practices today, that are based heavily on quantitative data, these early selection programs can appear rudimentary. However, we should acknowledge that breeding in the early part of the 20th century was a great advancement from the century earlier and it is at this point in history when many of the livestock breeds were moved to 'colonies', which later became major food producing nations, one of which would be Australia. Indeed, the genetic improvement in the recent century has been made possible by the stock developed by the forebears of animal breeding.

Early developments included the establishment of breed societies in the 'new world' and an exportation of genetics from the old world. Initially, genetic improvement was focussed around bringing the best genetics into the new world and this was facilitated through the establishment of breed societies. The establishment of herd books within breed societies provided a way for buyers to verify the 'purity' of the stock they were purchasing, as the newly imported breed was an advancement over the local alternative, and it was this preservation of purity that was the main goal. Genetic advancement was achieved through a replacement of 'local' stock with 'improved' stock or the displacement of one breed with another.

Prior to the widespread use of artificial insemination, breeding was also a local affair. Since breeding was based in part on selection of a desired 'type', often set as a breed standard by the societies, the placement of stock in classes at exhibitions developed as an important ranking tool. Producers looking to advance their stock would seek out champions from an exhibition and the larger the exhibition (competition), the better the animal. However, the relative merits of producers in their ability to prepare animals for showing (eg feeding, grooming) may have been difficult to disentangle from genetic merit. Nevertheless, this culture of commerce supported a vibrant exhibition industry with local, state and national exhibitions. The remnants of these still exist today and some are still a marketplace for trade for some species, examples would be the Sydney Royal Easter show or the 'Ekka' Royal Queensland Show, to name a couple. These exhibitions were an important avenue for breeders to market their genetics. Without artificial insemination, commercial producers needed to purchase a natural service sire and a commercial producer's local genetics supplier was more likely to be a 'neighbour' in relative terms.

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THE RISE OF CORPORATISATION

The selection, marketing and trade of genetics today is very different to how it looked 50 to 100 years ago. The argument put forth in this paper is that this transition from a family enterprise, with a local selection and marketing program, to a more global corporate enterprise is based around four primary factors:

1. Reproduction rate
2. Production cost per breeder
3. Availability of reproductive technologies.
4. Ease of preservation and shipment of semen, embryos and stock

Progress in these four areas has created the corporatisation of breeding in some species more than others. These factors are contrasted across four species in Table 1 with indicative levels indicated for each. By comparing the corporatisation in these species and the contributing factors, we can make more informed predictions about how new technological developments may affect corporatisation in different species in the future.

Table 1. Indicative[*] levels of key factors leading to corporate investment in animal breeding programs across four major species

	Laying Hens	Pigs	Dairy Cattle	Merino Sheep
Reproductive rate	XXXXX	XXX	X	X
Low production cost per Breeder	XXXXX	XXX	X	XX
Availability of reproductive technologies.	XX	XX	XXX	X
Preservation and shipment of semen, embryos and stock	XXXXX	XX	XXX	XX
Hybridization, line crossing	XXXXX	XXX	X	X

[*] the more X's, the higher the level and contribution towards corporatisation of breeding programs

Let's first focus on the laying hen, where the reproductive rate is high, with each hen capable of laying 300 eggs per year, and a hen is low cost to maintain and support. A single corporate entity can finance the infrastructure to produce large quantities of commercial stock in a pyramid system. Also, although artificial insemination is somewhat limited to fresh semen, this provides little impediment to progress since considerable stock can be located in one facility. The fact that hatching eggs or newly hatched chicks can be shipped nationally and internationally at low cost also supports the corporatisation of breeding in that species. Finally, following the success seen in corn breeding, the development of inbred lines (which are crossed to form hybrid commercial stock) was a game-changer in the poultry industry. This could only really be achieved on a large scale with many lines of sufficient size, and this is where the corporate breeders pulled away from the smaller private enterprises in the last half of the 20th century. This same hybrid model was tried in other species such as pigs and beef cattle, to capitalize on the same 'hybrid vigour', but these attempts largely failed as the cost to maintain inbred lines was simply too high at the scale required. Also, these mammalian species lines that failed due to poor reproductive rates, as a result of the inbreeding depression, contributed to the downfall of these attempts. Similar to hybrid corn, these commercial birds were of limited value to keep as replacement stock by the commercial farmer, which means the commercial producer must keep coming back to the corporation for commercial chicks, which perpetuates the corporate model.

Within the scope of species considered for comparison in Table 1, pigs are next in line for the most corporate breeding model. Although the reproductive rate is much less than chickens, at 20-30 pigs per sow per year, they are far ahead of cattle and sheep that are naturally limited to one or a little over one progeny per year in natural mating situations. As a litter bearing species, the advantages of embryo transfer offer fewer gains than cattle and are less successful. The use of artificial insemination is widespread with the ability to ship fresh semen widely within a country. However, international shipment of stock and semen is limited by health status within some countries, with Australia restricting importation of new genetic material. Although the cost of maintaining a sow is considerably more than a hen, the intensive nature of swine housing in modern production practices enables large numbers of animals to be maintained with a moderate outlay of capital for land, which tends to be the limiting factor with more extensive species. This combination of factors has made the global swine breeding industry the next most corporate within the examples presented. Factors such as the cost and health restrictions to ship stock around the world has limited this corporatisation and as a result we find many more pig breeding companies, in more countries, compared to poultry. The cost of maintaining lines and perhaps challenges with inbreeding in a mammalian species has made the hybrid model that was successful in poultry infeasible in pigs. As a result, commercial pig rearing is dominated by dedicated lines that come together in a dedicated crossing program to produce commercial sows and feeder pigs.

Dairy cattle are the next most corporate of the species presented and this has been enabled through the widespread use of artificial insemination and the characteristic of essentially sex-limited breeding goals. Excellent conception rates from frozen semen and non-surgical techniques have allowed artificial breeding to become the standard in most developed dairy breeding industries world-wide. This has allowed global breeding businesses to be built around the sale and distribution of bull semen. The impact of artificial breeding is best realised when one answers the question "What would the dairy breeding industry look like if artificial insemination was never invented?". It is likely that without artificial insemination, that the dairy breeding industry would look a lot more like the beef or sheep industries, with many breeders and a structure that is much less 'corporate' by nature. Looking back at the dairy breeding industry in the 60's, before artificial breeding was widespread, the industry did indeed look more like the beef industry, with many more stud breeders selling bulls for natural service. Hindered by reproductive rate, crossbreeding of any kind has seen limited implementation, with the majority of cattle being milked commercially in the world's largest dairy producing nations being purebred, with New Zealand being a noted exception to this rule.

Finally, Merino sheep is the example of the species that is the least corporate, with many studs in operation and the primary market being the sale of rams for natural service matings. This is despite the ease with which semen can be stored; but perhaps reflecting the greater difficulty of AI (surgical) for ewes and the relative cost of AI compared to the value of the animal. Although Merino sheep was provided as this example, beef cattle breeding will share many similarities with sheep, but beef cattle has a greater degree of corporate influence. A notable difference with beef cattle is the more prominent availability of frozen semen and a viable export market. The export markets and channels in place to support the sale of dairy semen has been leveraged for beef semen sales globally. Also, unlike Merino wool production, where Australia dominates, beef production is a more global industry. This global aspect results in more corporate activity around semen purchase and sale.

Although crossbreeding is not common within a wool production system it is common in terminal and maternal sheep breeding (McMillan *et al.* 2023). The increased reproductive rate in sheep compared to beef, and the potentially reduced generation interval when ewes are lambed at a year of age, does promote greater implementation of cross and composite breeding systems in sheep than in beef cattle. This multi-breed nature of the breeding industry in sheepmeat productionhas enabled a national multi-breed genetic evaluation under Sheep Genetics in Australia (Brown *et al.* 2007), where beef cattle evaluations through BREEDPLAN in Australia have been dominated by within-breed evaluations as a result of the structure of the data coming primarily from breed societies.

CHANGING BREEDS

The change in breeds used over time has been dramatic in some instances. Take the Holstein-Friesian as an example, where it has dominated much of the developed world. The explosion of this breed began in the latter half of the 19th century at a time when farms were getting larger and milk supply and marketing moved to a more pooled system, with less scope for individual attributes. Changes to how milk was marketed favoured the Holstein and this displaced breeds such as Jersey, Guernsey and the Milking Shorthorn, that had an advantage for butterfat.

The change of breeds in the Australian beef industry has been even more dramatic in the past 30 years, as depicted in Figure 1. Presented is the population of registered cattle through the Australian Registered Cattle Breeders Association (ARCBA). Although this is not a perfect picture of the breeds in the commercial industry, it is logical to consider these numbers as a good indicator of change at a population level. The most remarkable change has been the move from an industry dominated by Hereford genetics to one dominated by Angus. The reason for this change cannot be proven but there are a number of theories. Considering the breed differences identified in America at the USDA Meat Animal Research Centre (Kuehn and Thallman 2022), the Angus breed is a clear leader for marbling, a product differentiator in many branded markets, one of which is Certified Angus Beef (CAB). CAB has grown into the world's largest beef brand, marketing over 1 billion pounds of beef annually (American Angus 2022). Although CAB is a brand that dominates in America, this same success paves the way for Angus brands operating in Australia as well. Secondly, the Angus breed leads for calving ease, making it a more solid choice for crossbreeding, especially when mating heifers. Some trait advantages, the rise in feedlot finishing in Australia and the associated access to key branded products are likely reasons for this rise in Angus over this time period.

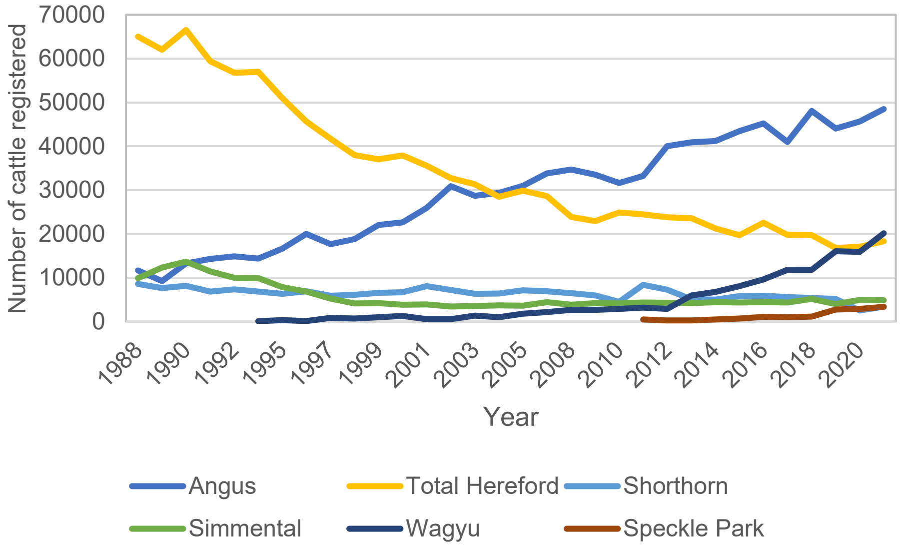

Figure 1. Changes in number of registrations of some beef breeds in Australia overtime
Source: Australian Registered Cattle Breeders Association (2023)

The total registered cattle population has fluctuated considerably overtime from a minimum of 127,000 in 2003 to 177,000 in 1990. Overall, the population is declining, where a linear regression estimates a decline of 513 animals per year in total registrations across all breeds. This gradual decline means that an increase in one breed is almost certainly gaining market share from another. Perhaps even more remarkable has been the rise of the Wagyu breed in Australia. This breed is also targeted at a premium market and lot feeding production system. The year 2000 was the first year to register over 1,000 Wagyu, and now Wagyu is the second largest breed for registrations, surpassing Herefords. It is remarkable to think that such dramatic changes in breed use is still taking place. The reason for this rise in Wagyu is likely to be similar to Angus, with a drive from the commercial market for a specific product, which in this case is one of very high marbling.

Changing the breed structure of an industry is perhaps the most dramatic example of genetic change. Changing breeds is certainly genetic change, but is it genetic progress? As animal breeders, much of the effort is focussed on within-breed selection in many instances, with very little input in the choice of breeds. This is despite breed choice having potentially the largest impact. The germplasm evaluation program at the USDA (Kuehn and Thallman 2022) and the recent Southern Multibreed project (Walmsley *et al.* 2021) in temperate Australia, along with Repronomics^{TM} in Northern Australia (Johnston *et al.* 2017) are meant to provide benchmarking for a limited set of current, more popular breeds.

In 1988 the Angus breed had a similar number of registrations to both Simmental and Shorthorn. Over time, Simmental and Shorthorn has retracted and Angus now registers 10-fold the numbers of either of these two breeds. The Speckle Park breed first registered animals in Australia in 2011 and has risen rapidly to now register a similar number to the Shorthorn breed. Clear objective information on the merit of the Speckle Park breed is not available. Although it might be seen as old fashioned, it would seem that objective comparisons of breeds is required for breeders to make informed choices on breed selection, as it continues to be in a state of change.

PERFORMANCE RECORDING AND THE BLUP ERA

It would be short sighted to suggest that performance recording started in the middle of the 20th century, as there has been recording of measurements for production and parentage going back well before that. However, it is during this period that more formal performance recording schemes were developed on a state and national level. Here in Australia, one such scheme was the National Beef Recording Scheme (NBRS) and there were similar schemes in other species in Australia and around the world. This was an era when phenotype truly was 'king' as it was the determining characteristic for selection. Then in the late 1980's and into the 1990's, schemes around the world transitioned to taking these performance databases and combining these with pedigree, that was typically recorded through a breed society, to create Estimated Breeding Values (EBVs). The technology to enable this was based on ground-breaking work (Henderson 1973) and Australia rapidly implemented these techniques (Graser 1982; Graser and Hammond 1985; Graser *et al.* 1987). At that time, the calculation of EBVs was brand new and required special skills in programming relatively large computational problems. Also, these problems required considerable computer power to run and such computer power was somewhat rare to access. These requirements resulted in the development work for EBV programs to be centred around Universities as they typically had the expensive computer hardware and the skilled staff required. The Animal Genetics and Breeding Unit (AGBU) at the University of New England, established in 1976 is one such entity. Around the world this race to implement EBV technology is what made the strong institutions in animal breeding that went on to make a significant impact in this area.

DAWN OF MOLECULAR GENETICS

During the mid-1990's, as EBVs were becoming entrenched, the next selection tool from the field of molecular genetics was also advancing. The future of animal breeding was in question. Was the calculation of breeding values using performance and pedigree information going to continue, or would this approach by surpassed with a purely molecular approach? Thoughts at the time were that once the genes controlling the traits were identified, selection could simply be to fix the desired variants. This was the beginning of somewhat of a divide in the field with two streams, Animal Breeding (quantitative) or molecular genetics. Those in the field of animal breeding did not simply bury their heads in the sand, but did what all good animal breeders do, and when faced with a lack of data, they 'simulated' what breeding would look like with molecular data and how the evaluation models would change to handle it. Some important papers resulting from this period related to the transition to molecular based breeding are Fernando and Grossman (1989) and Nejati-Javaremi *et al.* (1997).

Coming into the turn of the century it was becoming clear amongst the animal breeding community that molecular markers could have a significant role to play in practical breeding programs. 'Major genes" as they were commonly referred to at that time were starting to be identified. Some examples discovered included those affecting beef tenderness, including the related Calpain (Page *et al.* 2002; Casas *et al.* 2009) and Calpastatin genes (Schenkel *et al.* 2006) in this complex. The challenges facing the breeders was then how were we going to incorporate these new molecular tools into breeding programs? One early example of the integration of molecular information into breeding programs was the implementation of the Calpastatin genotypes in the Australia BREEDPLAN Brahman genetic evaluation for tenderness (Johnston *et al.* 2009). This was a challenging time for the animal breeding community as their funding sources were starting to fragment. Those wanting to fund genetic improvement in livestock were faced with a decision of funding the traditional programs that had been successful so far, or to start to direct money to this developing field of molecular genetics that just seemed more 'modern'. Unlike the field of quantitative genetics, that had been relatively low cost to date, research including genotyping and related laboratory costs was considerably more expensive. The result was animal breeders went through a phase where it was hard to secure research money unless their programs included something 'molecular'.

The first half decade into the twenty first century was one of very rapid advancement. Using beef cattle as an example, many molecular variants were being identified that were associated with economically important traits and companies were popping up that were now marketing these directly to farmers. Animal breeders found themselves sometimes in a position of validating these variants with independent data (Schenkel *et al.* 2005; Van Eenennaam *et al.* 2007; Johnston *et al.* 2010). In some cases single SNP tests were being sold for $80 USD. This quickly changed as more variants were discovered and genotyping companies realized that traits were influenced by multiple genes. The number of SNP in a test were quickly rising and were becoming limited by genotyping technology with plexes of 384 SNP being developed and sold. Meanwhile, alongside all this development of specific gene tests the animal breeding community was continuing to work on how this information would best be used and a landmark paper was released. This paper outlined the premise for what later became known as 'genomic selection' (Meuwissen *et al.* 2001). In 2005, while the search for specific variants continued to rage, a new genotyping array technology from Affymetrix (www.affymetrix.com) became available that enabled 10,000 SNP to be genotyped at reasonable cost, comparatively speaking. This technology was made possible by the Bovine Genome Project (Bovine Genome Sequencing Consortium 2009) along with contributing projects such as the Bovine HapMap project (Bovine HapMap Consortium 2009). With the ability to genotype large numbers of SNP effectively, the methods of genomic selection could then be applied. The 10K Affymetrix chip, ground breaking at the time, was soon replaced by the Illumina 50K (Matukumalli *et al.* 2009) with early access for research starting at the end of 2006, at an approximate cost of 300 dollars per sample, which was a dramatic reduction in cost per SNP, but is 10-fold the cost of genotyping today.

THE GENOMICS ERA

The 'standard' 50K chip changed the future of animal breeding and was a real turning point. During the next few years many changes occurred. The first was somewhat of a dissolving of the lines between quantitative animal breeding and molecular biology. Now instead of chasing individual genes, animal breeders could genotype their reference herds for 50K SNP and undertake meaningful Genome-Wide Association Studies (GWAS) analyses. This proliferation of large scale GWAS also discovered a number of new major variants. Genotyping companies were facing a cross roads, was the future bigger and better custom panels of hundreds of significant SNP, or were these mathematical approaches that use all 50K SNP, with no regard for which were significant, going to be better? Given the investment in specific panels (in beef cattle for example) to date, it seemed hard for the genotyping companies to believe the 50K shotgun approach could possibly be better. The length of time these debates raged was a blip on the overall timeline as the dairy industry soon proved beyond a doubt how powerful genomic selection could be (VanRaden *et al.* 2009). Where genomic selection was first applied I am sure is hotly debated, but I know it was applied in Canada in 2009 and although this may not have been the first implementation, it was not likely very far behind. The reason the dairy industry could apply genomic selection quickly was their extensive use of artificial insemination and long-standing progeny testing schemes provided them with a source of DNA (frozen semen) on thousands of bulls with highly accurate proofs, providing an instant genomic reference population.

The beginning of the second decade of the 21st century now saw other species looking at the success of genomic selection in the dairy industry and strategising how they could harness this same success. The key ingredient was clearly the reference populations and it was evident that these needed to be large and the bigger the better. The genotyping companies were also faced with the realization that their Intellectual Property (IP) in terms of specific marker panels could be displaced with this 50K product, something that was available to all. The implementation in dairy provided a stark example of a highly successful genomic product where genomic companies had no IP ownership. During this period the availability of low-density panels, first 3K, then 7K brought a new technology to the table in imputation (Sargolzaei *et al.* 2014; Browning and Browning 2016). Although the low-density panels did not last long as the cost of 50K genotypes came down, as global genotyping rates went up, the tool of imputation would prove important for the long-term.

The early implementations of genomic selection were predominantly multi-step approaches where predictions from the markers were combined with the traditional EBV, based only on phenotypes, in a blending approach. A popular blending approach used was the method of Harris and Johnson (2010) as applied to Australian beef cattle and sheep evaluations as described in Swan *et al.* (2011). In beef cattle, an approach applied in American Angus, as one example (Miller *et al.* 2018) was to bring the marker information into the genetic evaluation via a correlated trait with a heritability close to 1 and a correlation with the target trait in proportion to the prediction accuracy of the genomic trait (Kachman 2008). The multi-step approach allowed an expedited path for genomics to influence existing EBV procedures already in place bringing the technology to market with little delay. However, the multistep procedures were not optimal and relied on calibration steps that needed to be kept up to date (Johnston *et al.* 2010). The development of single-step procedures (Misztal *et al.* 2009; Aguilar et al. 2010) was a great advancement and allowed a simpler, more elegant approach, eliminating the need for separate calibration steps and enabled prediction with all the contributing information such as genomics, pedigree and performance information in a single procedure. In Australia, Sheep Genetics analyses went to Single Step in 2016 (Brown *et al.* 2018) and the first BREEDPLAN analyses transitioned to Single Step in 2017 (Johnston *et al.* 2018).

The implementation of genomic selection has been heralded as the greatest advancement in dairy cattle breeding since the widespread implementation of artificial insemination with frozen semen. Prior to genomic selection becoming fully implemented it was predicted that the rates of genetic progress would double in dairy cattle as a result of genomic selection (Schaeffer 2006). This has now been proven to be true (Scott *et al.* 2021; Fleming and Van Doormaal 2022). The early prediction of increased genetic progress by Schaeffer (2006) turned out to be an underestimate, possibly due to the fact it was based on early results with the Affymetrix 10K, whereas implementation has been with the Illumina 50K with more markers. Although higher density chips were also available at the time, these did not prove to increase the accuracy of genomic prediction.

Genomic selection has been a game-changer throughout many livestock industries. However, the basic implementation has not changed since it was implemented over a decade ago. Although there are some different variations being implemented, the basic model is via GBLUP, which is simply a better pedigree. In the past decade there has been much effort to increase genomic prediction accuracy through a better understanding of the genome. This era coincided with a great increase in whole genome sequencing resources being generated. The highly successful 1,000 bull genomes project (Hayes and Daetwyler 2019) is one example. Implementing sequence variants in the genetic evaluation has not increased selection accuracy considerably as demonstrated in dairy cattle by VanRaden *et al.* (2017) and in sheep by Li *et al.* (2021). The lack of papers purporting increases in selection accuracy following all the sequencing being done around the world at the recent (July 2022) World Congress on Genetics Applied to Livestock Production in Rotterdam (2022 WCGALP) was a testament to the disappointing progress in this area. The potential increase in prediction accuracy through models that more closely match the function of the genome still remains and should be pursued.

IMPACT OF GENOMIC SELECTION

Presented in Figure 2 are the genetic trends in Australian Angus, Friesian and Merino for a major respective economic index, each standardized to a genetic standard deviation. The increase in genetic progress in dairy is clearly evident in the graph, coinciding with the implementation of genomic selection in Australian Friesian in 2012 (Datagene 2022), and earlier for some other countries influential in dairy cattle genetics. In fact, a linear estimate of the trend 2001-2011 compared to 2012-2021 indicates the trend increase is over 4-fold in Friesian. The Merino trend is also increasing post-genomics with an increase of 1.57-fold pre and post genomics, which was first implemented in 2013 (blending Swan *et al.* 2011) with single step implemented in 2016 (Brown *et al.* 2018). The increase in trend in Angus is less dramatic with a 1.17-fold increase before and after the implementation of genomics in 2011 (blending) with single step implemented in 2017 (Johnston *et al.* 2018).

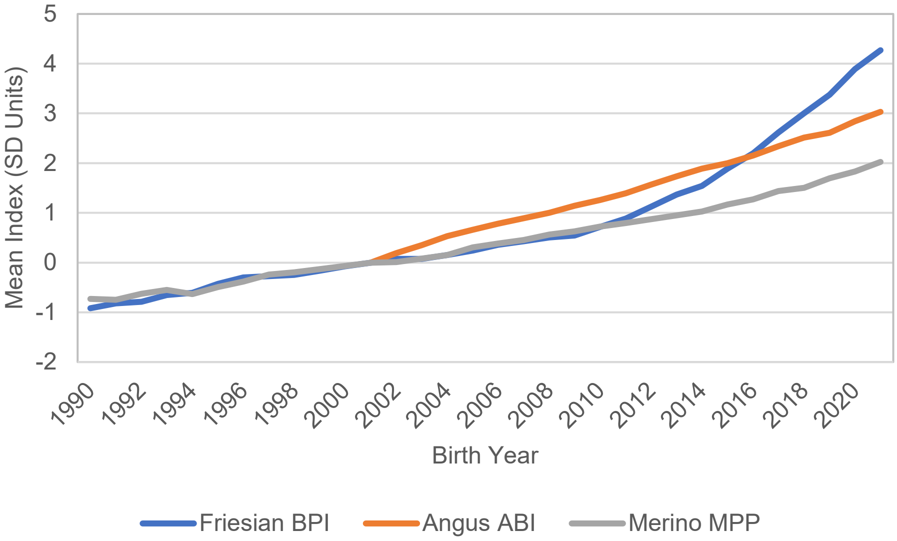

Figure 2. Standardized genetic trends for a prominent economic index in Australian Friesian, Angus and Merino populations
Source: Datagene, Angus Australia and Sheep Genetics (2023)

The dairy industry capitalized on genomics by greatly decreasing the generation interval on the male side, as sires no longer needed to be proven for lactation related traits through their daughters. The selection accuracy for females also greatly increased and was no longer plagued by preferential treatment of ‘bull dams’. In contrast, the generation interval in Merinos and Angus could not be reduced to the same degree, as many of the economically important traits are measurable on the sire himself, promoting the use of young sires. In the case of Angus, carcass traits required progeny proving to some degree but ultrasound on the yearling bull was also available as a highly correlated predictor (Reverter and Johnston 2001), and similarly wool traits are measurable on young rams. Despite the already heavy use of young sires in Angus, Miller (2023) showed how the average age of sires is reducing in American Angus post the implementation of genomic selection.

Although the impact of genomic selection is starting to show in Merino and Angus, the results are far less dramatic than in dairy cattle. Despite biological differences such as generation interval and the levels of AI etc., it is reasonable to expect that there is much opportunity to further increase progress with the technology for both sheep and beef. One focus area could be the continual increase in selection accuracy that may be possible with further increases in the size of the reference population, which will accompany increases in genotyping, as long as breeders keep up the recording effort. One difference between dairy cattle breeding compared to sheep and beef cattle is that large breeding corporations have a much greater influence in dairy cattle breeding, compared to sheep and beef cattle. These large corporations run what is closer to a single-desk decision making process, compared to the thousands of decision makers in sheep and beef cattle. These same companies are able to hire specialised talent in the way of Ph.D. geneticists and implement the latest tools in selection. This rise in the corporate domination of breeding companies in dairy cattle globally was outlined by John Cole as part of the 2022 WCGALP plenary (no reference available). It was suggested that such companies will likely move to a more isolated model, with custom evaluations and reference populations and a potential withdrawal from industry wide evaluation schemes such as that provided by Datagene in Australia.

NEW TECHNOLOGIES AND A MORE CORPORATE FUTURE

Sheep and beef cattle breeders in Australia should be looking at the greater progress experienced in dairy cattle as an illustration of the potential threat to their business models. How would they compete with a large corporate breeder that is employing the tools available, such as genomic selection with custom reference populations and novel traits, and large-scale in-vitro embryo production programs with embryo genotyping? It is the suggestion of this paper that the reason why large companies have not entered this market is because of the lack of a technology, such as the deployment of artificial insemination in commercial farms, that is the major inhibitor. There is one technology on the horizon that has been in development for a number of decades and is described as a 'surrogate sire' in the review of reproductive technologies and their impact on genetic improvement by Mueller and Van Eenennaam (2022). This surrogate sire can be described as a walking artificial insemination delivery, where a natural service sire is breeding cows, but delivering the genetic material from an elite sire. This technology could provide the step change in technology needed for a significant entry of corporate investment into the largely untapped sheep and beef cattle genetic supply markets. Collectively this could be a very significant market for commercial genetics companies. There are about 10 times as many beef cattle as dairy cattle in Australia alone. The other advantage of this walking artificial insemination model would be the opportunity to disconnect the genetics of the walking bull from the genetics he is passing through his semen. This could be quite opportunistic for regions like northern Australia, where the sire will need to be adapted for the harsh tropical climate, but the resulting calves could be more suited to a feedlot system. A potential example could be a walking Brahman or tropical composite sire delivering elite Wagyu genetics.

Clearly the deployment of reproductive technologies can be transformational. A more recent technology that has had a large impact has been sexed semen as deployed in cattle breeding internationally. This has had recent significant ramifications for beef production in many countries, especially those with well-developed beef and dairy sectors. As outlined in Miller *et al.* (2021) sexed semen has created a significant increase in beef cross calves from the dairy herd, often referred to as 'beef on/from dairy'. Several factors have come together to facilitate this, among which is the availability of sexed semen, allowing dairy farmers to target dairy female replacements from the best cows in their herds and breed the remainder of the herd to beef sires to maximize their value. This trend was exacerbated by low global milk prices and a shrinking dairy herd, which decreased the demand for dairy replacements.

A step change in this 'beef on dairy market' could be possible with an improvement in embryo production. If a calf with half beef breed heritage is more profitable than a dairy calf, then a pure beef breed calf would be even more valuable. To accomplish this, bottom-end cows that are getting mated to beef semen could become pregnant with a pure beef embryo instead. At the moment, the cost of generating these embryo's and their decreased conception rate must make this proposition economically unattractive or it would have taken off. One pipeline that could be exploited would be the generation of IVF embryos from slaughter females. These could be culled beef cows, or slaughter heifers from feeding programs without drugs that prevent oestrus, which are purported to create difficulties in creating viable embryos. If commercial genotyping was widespread, the genetic merit of these females could be made available and linked to their mandatory national electronic ID in many countries. These best commercial females could be a source of the 'beef from dairy' animals, or even replacements in beef herds. The viability of replacements in beef herds would then depend on the specific herd genetic merit, the merit of the embryos and the increased costs per live replacement generated through embryos. The use of sexed semen could target females for replacements and males for dairy-beef as required. Another parallel application would be the production of more high value beef genetics from tropical environments. Similar to the surrogate sire scenario presented earlier, a well-designed beef embryo could lift the value of the calf generated from this system, with calves placed in easier finishing systems such as feedlots, while maintaining the indicus content required in the females.

Another step change in technology that could forever change animal breeding would be the realization of what is referred to as speed breeding. This was referred to as *In Vitro* Breeding (IVB) in the review by Mueller and Van Eenennaam (2022) and new breakthroughs to support this approach were recently reviewed by Goszczynski *et al.* (2019). The technique is called speed breeding as the generation cycle can be reduced to 3-4 months in cattle. Multiple embryos can be generated from elite parents and these embryos can be the start of multiple embryonic stem cell lines (ESC). The multiple ESC can be genotyped and through genomic selection, the best ESC can be selected. With viable gametes possible from ESC, the best ESC can be joined to create another generation of embryos, which will start another generation of selection. This technology, if implemented on a large scale, could create further opportunities for large corporate breeding companies, especially when combined with walking artificial insemination as previously described. Considering factors related to corporate investment in breeding as outlined in Table 1, walking artificial insemination allows genetics to be dispersed widely and speed breeding reduces the cost of maintaining the breeding female, as much of it will be done in the lab. Also, to undertake the breeding at a large scale will require investment in lab facilities. Currently in species such as sheep and beef the breeders with the land required to maintain the breeding herd dominate. Speed breeding could open this market to those with the capital to invest in lab facilities and is less tied to land ownership.

As genomics has shaped developments over the past two decades it is certain to continue to play a major role. It is making enabling technologies such as reproductive technologies more productive, which will also increase the corporatisation of breeding as outlined in Miller (2023). The cost of genomic sequencing continues to decline. Twenty years ago there was the push for the 1,000 dollar genome and this has been passed (NIH 2023) and the new horizon is a 100 dollar genome (Illumina 2023). With sequencing costs continuing to decline, genotyping by sequencing is poised to offer a low-cost genotyping alternative that is already being deployed (Snelling *et al.* 2020; McEwan *et al.* 2021). Such low-cost genotyping could also open up the market for widespread commercial genotyping. In beef cattle this could mean a genotype on every animal in key supply chains. A scoping study on the widespread use of genotyping in the Australian red meat industries for traceability purposes found that the biggest advantages to genotyping every animal would be the opportunities for supply chain efficiencies and better adoption of genetic improvement tools (Banks *et al.* 2022). Widespread commercial genotyping could change how reference populations are developed with a shift away from a seedstock focus to more dedicated commercial streams, that could be more private. This availability of private reference populations, with custom data collection streams, including novel traits, could also fuel a rise in more corporate breeding investment.

CONCLUSIONS

Animal breeding has gone through some transformative change in the past 50 years. From performance recording to BLUP and now genomic selection, advanced breeding programs today are making more progress than ever before. These improvements have not all come from the animal breeding community but in many cases development in other fields have been leveraged and successfully implemented. The development of large-scale performance recording schemes and genetic evaluation was made possible through the parallel developments in computing power. Advancements in reproductive technologies have played an important role in shaping industry structure including the rise of corporate ownership. Genomics was made possible through the development of low-cost, moderate density genotyping, following developments created for human genetic applications. Similarly, future opportunities are sure to leverage new technologies such as low-cost sequencing applications to reduce the cost of genotyping. Advancements in genetic engineering could make in-vitro breeding or the deployment of surrogate sires available on a commercial scale. These are technologies that could change the rate of genetic progress and also the structure of the industry, with a likely increase in corporate ownership. As new technologies continue to be deployed, new opportunities are created for more structured corporate ownership, which will continue to change the animal breeding industry as we know it.

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