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Evolution of Genetics Organisations' Strategies through the Implementation of Genomic Selection: Learnings and Prospects

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Abstract: Since its initial description in 2001, and with falling costs of genotyping, genomic selection has been implemented in a wide range of species. Theory predicts that the genomic selection approach to genetic improvement offers scope both for faster progress and the opportunity to make change in traits formerly less tractable to selection (hard-to-measure traits). This paper reports a survey of organisations involved in genetic improvement, across species, countries, and roles both public and private. While there are differences across organisations in what have been the most significant outcomes to date, both the increased accuracy of breeding values that underpins potentially faster progress, and the re-balancing of genetic change to include real progress in the hard-to-measure traits, have been widely observed. Across organisations, learnings have included the increasing importance of investment in phenotyping, and opportunities to evolve business models to engage more directly with a wider range of stakeholders. Genomic selection can be considered a more modular approach to genetic improvement, and its simplicity and effectiveness can transform both genetic improvement and the effectiveness of multi-disciplinary approaches to improving livestock and plant production, enabling potentially very significant increases in agricultural productivity, profitability and sustainability.



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1. Introduction

The core tools, or knowledge domains, deployed in all agriculture are genetics, nutrition, and management (including health considerations). To a large extent, Research and Development (R&D) and implementation have largely tended to proceed within these domains, albeit with often-stated goals of integration. The domains draw on separate types of knowledge, and this fact, coupled with limitations in scale and complexity of experimental design (reflecting the fact that R&D depends on investment of scarce funds) has tended to maintain the separation. Recent significant development in one area of measurement or data capture has transformed one of the three domains, and has begun to change how R&D can and does address the three domains and their integration. That development is the introduction of techniques for “reading” the genetic makeup of individuals—known as genotyping.

This paper explores how genotyping has been utilized from two perspectives: firstly, within the domain of genetics, and secondly, the way in which technology is changing how agricultural R&D is done, and what scope it can address. The introduction briefly describes the activity of genetics R&D and implementation, then outlines how potential applications of genotyping have been investigated, and the general principles of deployment. The central approach of this paper is then outlined: through structured interview with a range of practitioners of genetic improvement, common themes emerging through deployment in a range of species and for a range of goals are identified together with how strategies for genetic improvement are evolving. The paper then draws on the insights from those interviews and published results to consider how deployment of genotyping is changing agricultural R&D and its implementation.

The starting point for this approach is the genetics domain. In simple terms genetics in relation to agriculture is concerned with two effects: how choice of animals or plants from which to breed affects current performance, and how that choice affects performance in subsequent generations—this latter usually termed genetic improvement. Both choices (they can be applied in a single combined decision process) depend on identifying individuals with more favourable genetic make-up for some goal or goals. This simple description captures the “algorithm” of genetic improvement:

- define the goal—what aspects of performance or traits are important, and how we wish the change any or all of them: referred to as defining the breeding objective
- identify the individuals with superior genetic makeup for the breeding objective (i.e., for the traits in the objective): referred to as predicting breeding value
- selecting the individuals with superior genetic makeup and mating them in an optimal way to produce progeny

Harris and Newman [1] provide a comprehensive expansion of this algorithm.

While defining the breeding objective is the starting point of this approach, the second step has occupied the bulk of technical attention during the development of the theory and practice of genetic improvement over the last 7–8 decades. Individuals’ genetic makeup, or merit, can be estimated from using two types of “clues” [for the description “clues”, Brian Kinghorn, pers. comm.]—the relationships amongst them, based on known pedigree, and their individual performance, or phenotype, for traits of interest. Prior to 2001, the two significant developments in the theory of estimating genetic merit were selection index [2] and best linear unbiased prediction, or BLUP [3]. Both methods use phenotypic data, and where known, pedigree. BLUP offered advantages over selection index in accounting for genetic change through time, enabling use of heterogeneous data (both in phenotypes available per individual, and in pedigree relationships), and given appropriate relationship structure, unbiased estimation across multiple breeding units (such as flocks or herds, but extending to countries). BLUP methods were introduced into breeding programs in most livestock species in western countries from the 1980s, assisted by the increasing availability and price attractiveness of large-scale computing. Almost from the start of implementation, rates of genetic progress as estimated from the data increased in all species where BLUP methods were implemented (this is not to imply that progress had not been made prior to use of BLUP methods, but that it accelerated markedly).

The power of selection index and BLUP approaches were enhanced by the development of methods for utilisation of DNA data (genotypes), marked by the publication of the concept of genomic selection [4]. It is no exaggeration to say that this paper marks the start of a new, in some ways revolutionary phase in genetic improvement. Such description can be unfortunate where reality does not match “hype”, but the method has indeed transformed approaches to genetic improvement wherever applied. Meuwissen et al. [4] outlined the basic logic of the approach; Goddard and Hayes [5] provide clear explanation of the application. The present paper does not go into technical detail, but a brief description of the basic elements, and summary of aspects of the research that has grown from the initial paper, will underpin the focus here.

Genomic selection depends on the ability to “read” the DNA of organisms—identifying the nucleotides present in an animal at known locations in the genome. The locations being read are referred to as Single Nucleotide Polymorphisms (or SNPs), and the ability to read SNP genotypes has grown exponentially in the last two decades, measured as the price per SNP. The “reads” at each SNP location together comprise the genotype of the individual, and genotype maps now routinely include tens of thousands of SNPs, up to full DNA base sequence.

The second essential requirement for genomic selection is a sample of individuals from the population of interest that have been genotyped, and on which some measure or assessment of performance has been collected. The measure may be a trait(s) measured on the individual itself (its phenotype) or trait(s) measured on known relatives of

the individuals—for example, progeny groups. This group of measured and genotyped individuals is known as the genomic reference population.

With a genomic reference population established, it then becomes possible to genotype other members of the population, and look for similarity between their genotypes and those of the genomic reference population, and from that similarity infer the value of the genes of those individuals. To make the point very clear: the genomic reference is individuals with both known genotypes and measured phenotypes, and the remainder on the population (non-reference) can then be evaluated genetically from their genotype alone.

The size, and to a lesser extent the design, of the genomic reference population, is crucial in determining the accuracy with which genetic merit can be estimated for animals without phenotypes. This topic will be returned to later, but the key points in relation to that accuracy were covered by Goddard and Hayes [5]:

- accuracy of estimation of genetic merit (or breeding value) increases with increasing size of the reference population, but with diminishing returns to scale,
- accuracy of estimation of genetic merit (breeding value) is higher for traits with higher heritability,
- accuracy is affected by the level of relatedness of individuals within the reference population and between the reference population and the rest of the population—higher relatedness enabling higher accuracy, and
- the reference population needs to be maintained in terms of its relatedness to the current active population—for a population undergoing selection, the accuracy available from the reference population declines over time [6,7] (noting that drift and mutation will also contribute to reduction in relatedness over time).

Meuwissen et al. [8] set out the two opportunities presented by genomic selection:

- the accuracy of prediction of genetic merit that is possible, including for individuals with and without phenotypes, with increased accuracy providing scope for more rapid genetic improvement, and
- the decoupling of measurement and selection. This provides two sorts of opportunities:
 - to evaluate large numbers of individuals at the price of genotyping alone
 - to evaluate selection candidates for traits that cannot be measured on live animals or, or can only be measured some time after selection would ideally occur

Together these opportunities mean that genomic selection can be deployed to achieve faster genetic change in individual traits, genetic change in more traits simultaneously, or the two together, and enable screening of commercial populations to allocate individuals to their most appropriate management regimes and/or target markets.

At the time of the original paper [4], genotyping was not yet cheap enough for widespread implementation of genomic selection. Through the 2000s and beyond about 2008, this began to change rapidly, with the earliest wide-scale applications in dairy cattle. A major attraction there was in using genomic selection to evaluate young bulls, potentially replacing the longer and more expensive progeny testing systems that had been the basis of dairy cattle genetic improvement since the mid-1950s. Shaeffer [9] highlighted the potential cost-savings (92%) and increases in rate of progress (doubling) available, and almost immediately, dairy cattle breeding programs in the developed world switched to genomic selection. Since then, applications in other species has grown rapidly.

The concept of genomic selection has been termed a paradigm shift [8]. “Paradigm shift” refers primarily to the decoupling of trait recording and selection. The impact of the concept on the research community is evident in a Google count for the term “genomic selection”—163 million hits at 20 April 2022, compared to 2.4 million hits for BLUP at the same date. Similarly, the original paper now has nearly 5000 citations, compared to 1676 citations for the Henderson paper outlining BLUP [3]. These comparisons are not intended to imply relative merit—simply the level of engagement that genomic selection has generated.

This paper explores how a sample of practitioners have implemented genomic selection, what has been learnt to date, and how breeding strategies have evolved. A brief

overview of areas of research and development around genomics and in particular genomic selection is provided as background or context for focus on implementation.

Firstly, there have been a number of useful collections of articles discussing genomic selection, with that in *Animal Frontiers* (6(1), 2016) providing an excellent starting point. Recent proceedings of the World Congress of Genetics Applied to Livestock Production [10,11] extend the coverage enormously—over 1600 papers across two conferences, with a high proportion in some way utilizing or addressing genomics. An excellent review of the status of genomic selection covering a range of theoretical and implementation issues is Misztal et al. [12], and Verbyla et al. [13] provides an excellent outline of the steps involved in implementation of genomic selection at commercial scale, including the R&D and application phases.

Secondly, areas of research and publication include:

- Methods and tools for analysis of genomic data, both for genomic selection and more broadly for exploration of the genomic architecture of traits
- Theoretical and more recently experimental investigation of changes at the gene or SNP level under genomic selection
- Theory and tools for use of genomic data jointly for selection and management of genetic variation
- Design of genomic reference populations on both within- and across-population basis (where population can be breed, region or country of origin)
- Pre- and post-implementation scoping and reporting of implementation in a wide range of species, including animals (terrestrial and aquatic), plants, insects, and microorganisms
- Traits, and methods of phenotyping, including production (both output and input), product quality, health- and disease-related, metabolic, and behavioural traits
- and Evaluation of breeding programs for effectiveness and economic efficiency, including for economically and/or environmentally challenging situations

Thirdly, and of relevance to the broader agriculture context within which genomic selection is practiced and genomic methods are used in research, studies of genotype-by-environment interaction, and more broadly of how genetic and non-genetic (e.g., nutritional, or management) choices work together in value chains, e.g., [14]. These latter reflect a paradigm shift additional to that noted by Meuwissen et al. [8]: as genotyping becomes more and more cost-effective, and as genomic reference populations are built using a mix of specific-purpose populations and field data, genotyping can describe the genetic makeup of recorded populations where there are identifiable environmental or treatment differences, which enables greatly increased scale in experiments in fields where traditionally experimental size has often been limited.

2. Materials and Methods

The foregoing is intended as a general introduction to genomic selection. Of potential interest both to practitioners across species, and to a wider, non-geneticist audience, are the questions:

- how has genomic selection been implemented in practice?
- with what results so far and what impacts on how genetic improvement is being practiced?

A survey was conducted to help address questions related to genomic selection that are of interest to plant and animal breeders as well as to a wider, non-geneticist audience.

The broad questions were examined via structured interviews with a diverse sample of practitioners. Twenty-three different organisations are represented, and all interviewees provided a mix of written and verbal response to the following questions. The organisations were chosen to represent four broad roles within genetic improvement, and from the author's experience of publication by the organisations. They reflect a range of species and countries, but to be clear, all have implemented genomic selection to some extent.

For the Results and Discussion, the interviewees have been grouped. The grouping outlined is somewhat arbitrary, but reflects diversity in two dimensions of enterprises or organisations involved in genetic improvement:

- Whether single enterprise or business, or including or servicing multiple enterprises or businesses. For example, an individual beef cattle stud is likely to be smaller in economic scale (e.g., turnover) than a breeding company, even though the number of animals (females) in the breeding population being managed may be similar. A breed association will provide some set of services to multiple such enterprises.
- Whether directly involved in collecting data and/or making selection decisions, or providing services supporting such decisions. Breeders and breeding companies (or programs) are directly involved in such decisions, whereas breed associations and national genetic evaluation systems provide supporting services for those decisions.

This grouping does not map precisely to economic scale or scale of breeding program. For example, an individual beef cattle stud is likely to be smaller in economic scale (e.g., turnover) than a breeding company, even though the number of animals (females) in the breeding population being managed may be similar. A breed association will provide some set of services to multiple such enterprises, but may be no bigger, or even smaller, than some of its member businesses (studs).

The full listing of interviewees within groups, with links, is included in Appendix B.

The interviewees are only sampled from two of the four possible cells within this 2-dimensional matrix. The breeding company/project group includes both private and public sector organisations, and as will become apparent, there is a trend for breed associations and national evaluation systems to make direct investments into at least data collection—within this simple classification, a role of the decision makers.

The questions included in the survey were:

1. What level of adoption or utilisation of genomic selection, i.e., genotyping for prediction of genetic merit, has been reached in your organisation –perhaps simplest answered as what proportion of selection candidates are genotyped, and in the case of a multi-stakeholder situation, what proportion of breeders or producers are genotyping some or all candidates for selection?
2. Has your organisation assisted with the uptake of genotyping—for instance via contribution to the cost of genotyping?
3. Has your organisation reviewed or changed breeding goals or indexes either as part of a planned process of implementation of genomic selection, or simultaneous with it?
 - a. If so, has there been an increase in the number of traits being evaluated?
4. Has your organisation invested (or co-invested) in any specialised or designed phenotyping projects, either with members or separately?
5. Does your organisation provide any incentives for phenotyping, whether broadly or for specific traits?
6. Within the population you or your members work with, is there any evidence of changes of parameters of the response equation, such as:
 - a. Reduction in average age of sires
 - b. Increase in use of elite males and/or females via Artificial Insemination (AI) and Embryo Transfer (ET), partly or completely focussed on genotyped animals
 - c. Increase in average accuracy of selection (in a general sense, this could reflect the average accuracy of genomic BVs in animals in the population)
 - d. Increase(s) in rate of genetic progress, whether for some individual traits and/or overall merit index
 - e. Changes in direction or rate of change in particular traits (an example I will be discussing is that of eating quality (EQ) in terminal sire sheep in Australia—where previously the genetic trend was unfavourable, driven by genetic correlations between EQ and traits contributing to efficiency of lean tissue growth

(Lean Meat Yield or LMY), but now the availability of genomic predictions for EQ as well as for LMY has resulted in reversal of the genetic trend for EQ

7. Can you comment on whether, and if possible to what extent, your organisation has drawn on government or industry funds in any aspect of the introduction of genomic selection? Additionally, if you have, do you anticipate that continuing into the future?
8. Has your organisation changed its strategy as a result of or in response to, the introduction of genomic selection? If possible, can you briefly describe the key changes underway?

Interviewees were contacted directly by the author. It was made clear that no confidential information was being sought, and that no evaluation or comparison of responses, in the sense of an organization performing in some way better or worse than others, was intended. Interviewees had opportunity to review the manuscript prior to submission.

Interviews were conducted by teleconference, but were not recorded electronically—rather, notes of the discussion were taken by the author. These notes have been distilled to generate the material reported here.

3. Results and Discussion

For this section, the interviewees have been grouped as outlined in Materials and Methods. Responses to the questions are summarized by the four groups as defined in Table 1. Direct comment or quotation from individual interviewees is minimal here, but key points from discussion are included.

1. What level of adoption or utilisation of genomic selection, i.e., genotyping for prediction of genetic merit, has been reached in your organisation—perhaps simplest answered as what proportion of selection candidates are genotyped, and in the case of a multi-stakeholder situation, what proportion of breeders or producers are genotyping some or all candidates for selection?

Table 1. Classification of Interviewees.

	Single Enterprise	Multiple Enterprise
Decision maker	Breeders Breeding Companies/projects	
Decision support		Breed associations National evaluation

Breeders: The beef breeders interviewed are all now genotyping 100% of young animals prior to selection, with the genotypes submitted for genetic evaluation via the BREEDPLAN system [15]. This level was not arrived at immediately genotyping became available: in all cases, some initial trialling was conducted allowing comparison of genomically enhanced estimates of genetic merit (EBVs in beef cattle in Australia) with standard BLUP EBVs [16].

The sheep breeders interviewed are genotyping lower proportions of their annual drop of candidates than beef breeders, likely reflecting the higher relative price of genotyping in sheep compared to cattle (prices for genotyping are similar per animal, but the sale value of rams is approximately one fifth that of beef bulls). However, the breeders interviewed indicated that the proportion of their flock being genotyped is rising and likely to continue to do so.

Breeding Companies: All breeding companies interviewed are genotyping 100% of candidates, with the exception of Tree Breeding Australia, where the reference population is being built through extensive genotyping across generations and evaluation of the potential utility of genomic information. As with the breeders, companies did not necessarily move to 100% genotyping of candidates immediately the technology became available—some research and development or learning process was involved. As will be discussed later, this

in some cases included evaluation of different genotyping platforms and even development of custom genotyping assays or chips.

Breed associations: In the beef breeds interviewed, genotyping has reached high levels across their membership—broadly around 67–90% in young animals. While this information was not sought directly, there was an overall impression that adoption of genotyping was higher among larger breeders (i.e., in terms of numbers of animals and hence economic scale) within the breeds.

National evaluation systems: Observations varied between species and to an extent country. In dairy cattle, 100% of male candidates (i.e., young bulls) are now genotyped. Genotyping in females has grown more slowly, but an increasing proportion of “commercial” heifers—animals not automatically assumed to be likely to be dams of bulls—are being genotyped, reflecting increases in accuracy of genomic breeding values and the resulting increasing utility of such information in supporting management decisions. In beef and sheep, adoption varies widely between breeds in the countries represented, with a tendency for adoption to be higher and faster in breeds that have been more active users of science-based breeding methods and technologies.

Overall, adoption of genotyping for genomic selection has been quite rapid after initial trialing and research: not as dramatically as in dairy cattle, but rapid in terms of technology adoption in agriculture [17].

2. Has your organisation assisted with the uptake of genotyping—for instance via contribution to the cost of genotyping?

This question is really only relevant for breed associations and genetic evaluation systems. None of the breeds surveyed have offered any financial assistance with genotyping at the individual animal level, but all had negotiated pricing arrangements for their members with the genotyping providers.

In general, this was also the case with breeding companies and genetic evaluation systems, but a very important contribution has been made in almost all cases (breeds, breeding companies and genetic evaluation systems) via co-investment with breeders, and with industry and/or government, in R&D. Such R&D in broad terms has been aimed at establishing proof-of-concept while simultaneously building genomic reference data, and the assistance in most cases included subsidization of the cost of genotyping for breeders involved.

Extending this point, all the breeders (beef and sheep) interviewed had participated in such R&D, and their data has contributed to the relevant reference populations.

This R&D phase continues where new traits are under development: for example in Australian beef and sheep, large industry and government co-investment in phenotyping for methane output is underway, and similarly in the Australian dairy industry for fertility phenotypes via the GINFO project [18].

The challenge of maintaining appropriate levels of phenotyping, including for new traits, has become a significant strategic challenge for all the types of business consulted here, and approaches to meeting the challenge are under development [19].

3. Has your organisation reviewed or changed breeding goals or indexes either as part of a planned process of implementation of genomic selection, or simultaneous with it?
 - a. If so, has there been an increase in the number of traits being evaluated?

This question was included to address the proposition that genomic selection would enable more effective selection for hard-to-measure traits, which in turn could lead to adjustment of breeding goals. Across the interviewees, no organization has specifically reviewed or changed breeding goals as part of a planned process of implementation of genomic selection, but in essentially all cases, that implementation has led to new thinking regarding objectives and what traits could be important:

Breeders: Observations included an increased focus on some traits reflecting greater accuracy in EBVs for those traits, a desire to have more traits included in genomic evalu-

ation, and that review of breeding goal(s) and indexes was enhanced by the increase in accuracy of EBVs for some traits, leading to greater focus on them.

Breed Associations: Similarly, among the breeds interviewed, two noted that review of breeding goals and indexes was occurring simultaneous with implementation of genomic selection, and that the implementation was increasing breed focus on collecting sufficient numbers of phenotypes to support useful genomic breeding values. The other noted that while the reviewing of breeding goals and indexes is a regular activity, implementation of genomic selection has encouraged consideration of formally including traits in the breeding goal that had previously been considered “important but too difficult to do anything about”.

Breeding Companies: In general, implementation of genomic selection has allowed companies to shift emphasis in their breeding indexes more towards the balance implied by an already-defined breeding goal—in particular, to place more selection emphasis on hard-to-measure and/or low heritability traits. This is broadly similar to the observations for breeders and breeds, but noting that all the companies interviewed had formally defined breeding objectives that included traits not previously under strong selection pressure because of lack of data and/or low heritability. Although not a documented or objective reaction from those interviewed, there was a sense in the discussions that this re-balancing of selection pressure was something of a pleasant surprise—in essence, that genomic selection was in fact providing a benefit proposed theoretically, but not definitively proven anywhere prior to the implementation process.

National evaluation systems: The first observation for this group is that in almost all cases, some new traits were added to the routine evaluations as R&D generated sufficient phenotypes to enable genomic prediction. This in turn has led either to increased interest in or focus on hard-to-measure traits, informed simultaneous reviews of breeding goals or indexes, and/or stimulated revision of goals and indexes to explicitly incorporate new traits. An example of the latter is that Sheep Genetics now offers indexes that include Lean Meat Yield and Eating Quality breeding values, which have only become available via R&D and depend on genomic prediction for animals in ram-breeding flocks [Andrew Swan, pers. comm.] [20].

Extending this point, the changes—either rebalancing and/or introduction of new traits—have stimulated development of new extension tools and programs. These tools and programs have covered both new traits or indexes, as well as tools focused on genomic pedigree at the breed or across-breed level.

A more general observation relevant to this question is that in all four types of organization, implementation of genomic selection has stimulated more attention to the meaning and composition of breeding goals, and to the realization that expansion of breeding goals and introduction of new traits can be a conceptually simple and logical process. As this attention and realization grow, it seems likely to underpin quite considerable re-thinking of breeding goals, especially to include traits previously ignored as being too difficult to do anything about, and to incorporate traits relevant to more recent considerations, such as emissions and welfare-related traits [18,21]. To varying degrees, this is being actioned via more formal forward planning of R&D into potential traits and into phenotyping strategies, and into thinking much more deeply about the implications of, for example, more rapid change in fitness traits. This is somewhat analogous to new appreciation of the effectiveness of selection for disease resistance [22,23]—understanding that change in previously difficult traits can be much more effective than was thought should encourage broad and imaginative thinking about what a particular breeding program can realistically aim to achieve.

4. Has your organisation invested (or co-invested) in any specialised or designed phenotyping projects, either with members or separately?

Breeders: All breeders interviewed had participated in industry R&D programs involving collection of existing and/or new phenotypes, and genotyping. This invariably involved additional investment by the breeders, either via additional spending on recording

equipment, additional labour, and/or investment in genotyping animals that would not otherwise have been genotyped. All such R&D programs involved some level of industry and/or government investment.

Breed Associations: As with the breeders, the breeds interviewed had all participated in industry R&D programs, including making significant financial investments from breed funds.

Breeding Companies: Similarly, the breeding companies surveyed have all invested in specific phenotyping projects, but the level of external co-investment (from industry and/or government) varied considerably. There is a trend to investment in phenotypes being informed by definition of the breeding goals, and therefore evolving as the breeding goals evolve (see point 3 above).

National evaluation systems: All the evaluation systems consulted have either initiated and/or participated in specific phenotyping projects, usually for a combination of existing and novel traits, moving to focus on novel traits as the value proposition for genomic selection for existing traits has become established.

There has been no single approach to the design of such projects, although some focus on ensuring involvement of higher genetic merit animals or breeding units is evident [24].

5. Does your organisation provide any incentives for phenotyping, whether broadly or for specific traits?

Breeders: This question is not relevant to breeders as individuals.

Breed Associations: All breeds interviewed have taken initial steps to encouraging phenotyping, either related to specific traits, or as some reduction in charges for enrolling animals into genetic evaluation. One breed has started offering incentives for submission of phenotypes for traits not currently well-recorded.

Discussions indicated that strategies in relation to this issue are likely to evolve [18].

Breeding Companies: This question is not directly relevant to breeding companies, except where the company has contractual agreements with suppliers of data, where the contractual arrangements will reflect the value of the data itself.

National evaluation systems: Incentives for phenotyping have been offered (provided) by national systems in a range of ways, including assistance with the cost of genotyping animals in particular priority herds or flocks, and similarly but for herds or flocks meeting recording level or quality standards, discounts on standard evaluation charges in return for defined levels of phenotyping.

The incentives provided through these mechanisms have in most cases overlapped with, or been a component of, R&D programs, but several organizations have or are considering moving to incorporating such incentives in their normal charging schedules [e.g., CDCB, Appendix A].

6. Within the population you or your members work with, is there any evidence of changes of parameters of the response equation (with possible examples listed):

There was considerable diversity in responses and discussions on this question, not so much in terms of whether changes in parameters contributing to rate of genetic progress had occurred or been observed, as in what those changes were. In part this likely reflects the way the question was posed, with sub-questions relating to different parameters, in addition to any variation reflecting the different natures of the organizations interviewed. Recognizing this diversity, some overview points are presented first, before reporting on the responses of the different organization types.

Firstly, all interviewees commented on increases in accuracy of breeding values—mostly in relation to young animals, but also for traits for which breeding values previously had only low accuracy. An interesting example of the latter is adult traits in sheep—weight and wool production of females. As interest grows in controlling maintenance costs of breeding females in extensively managed species, ability to restrict increases in adult weight while simultaneously increasing early life growth rate (for slaughter progeny) becomes increasingly important. To date, limited recording of adult weights has meant that

these have simply increased as a correlated response to selection for early growth. This is a specific example of a more general issue of traits that for whatever reason have not been extensively recorded. Genetic evaluation of such traits (i.e., to generate estimates of genetic merit) has previously had low accuracy, limiting breeders' capacity to manage them genetically.

Secondly, and to varying extents, breeders are now making greater use of younger animals, reflecting increased accuracy of estimates of genetic merit for such animals. This has been most dramatic in dairy cattle breeding, where genomic selection has essentially replaced progeny testing schemes [9], but was commented on to some extent by all interviewees.

Thirdly, increases in either rate of genetic progress and/or rebalancing of genetic change across traits were most strongly noted in organisations with what seems reasonable to interpret as the strongest pre-existing focus on genetic improvement and breeding program design. For example, breeding companies with well-established and formally designed breeding programs (formally in the sense that detailed analysis of design options, including all steps in the breeding program design "algorithm" [1] most readily reported significant increases in either of these aspects. This was not so clear in the examples for beef and sheep, or for beef breeds, partly reflecting variation amongst breeders with multi-member organizations in their utilisation of genetic improvement methods and technologies.

Breeders: None of the beef or sheep breeders interviewed reported dramatic changes in rate of genetic progress, but did report what are likely early or leading indicators of significant acceleration: increased accuracy of breeding values in young animals including for hard-to-measure traits, and increased use of younger animals in reproductive programs (i.e., using Embryo Transfer on selected females). As confidence in genomic breeding values continues to build for these breeders, it seems likely that increased use of younger animals coupled with increases in accuracy across breeding goal traits will be reflected in significant acceleration of genetic progress.

Breed Associations: The general observation here was that to date there has been no "across the breed" increase in rate of genetic progress, but that early signs of change are apparent, and that there have been significant genetic changes in some specific traits introduced with the implementation of genomic selection. Retallick et al. [25] report examples of this for welfare-related traits in Angus cattle in the USA.

All breeds interviewed commented on increased extension effort through recent years, aimed at encouraging more effective use of genetic information amongst their members: this focus has coincided with the implementation of genomic selection.

Breeding Companies: Where the company interviewed had fully implemented genomic selection (as compared to being still in the process of trialing it), substantial increases in the rate of progress both overall and in hard-to-measure traits have been observed.

National evaluation systems: In broad terms, observations for the national evaluation systems reflect those for the other three interview groups: substantial acceleration reflecting reduced generation interval in dairy, considerable variation amongst breeders in the respective species—particularly beef, and increased response most noticeable in hard-to-measure traits. Examples of the latter which mirror the point noted above re welfare traits in US Angus, include:

- the dramatic change in genetic trend for traits related to meat eating quality in sheep in Australia [20], reversing previous unfavorable correlated responses to selection for growth and carcass leanness,
 - the equally dramatic reversal of genetic trends for fertility in dairy cattle, which while not solely due to implementation of genomic selection, have been enhanced by it [Paul Van Raden, Andrew Cromie, Matt Shaffer—pers. comm.]
7. Can you comment on whether, and if possible to what extent, your organisation has drawn on government or industry funds in any aspect of the introduction of genomic selection? Additionally, if you have, do you anticipate that continuing into the future?

Responses were consistent across the four groups: to varying extents, all had participated in (or initiated) R&D projects focused on trialing aspects of genomic selection, and receiving industry and/or government R&D funding. Typically, such funding assisted with genotyping costs, development of analysis tools and data analysis. As evaluation of the technologies moved beyond the “proof of concept” phase, external assistance has increasingly focused on assisting with phenotyping of novel traits, such as methane emission levels [Sam Clark and Julius van der Werf, pers. comm.], and organizations fund more routine phenotyping and genotyping from internal sources.

All organizations indicated that where industry and/or government R&D funding is available, for instance to assist with development of novel traits, it would be applied for.

8. Has your organisation changed its strategy as a result of or in response to, the introduction of genomic selection? If possible, can you briefly describe the key changes underway?

Responses to this question were richly diverse, and to convey this rich diversity as fully as possible, individual comments and observations are presented below, without identifying the individual source.

Breeders:

- Greater use of young sires, more data capture from multipliers, and development of new traits
- Having greater scope to control direction is invigorating, and we have developed better understand of both the technology and our choices, leading to increased confidence in what we are aiming for and doing
- There is greater urgency to identify traits that need to be recorded and included in the evaluation
- We are reviewing our business structure aiming to get the best out of the technology
- We are developing new product lines—and can do so rapidly with genomics; and moving to having a genotype-only multiplier tier in our business
- We are focusing more on potential new traits, especially around easy care attributes and fertility

Breed Associations:

- Genomic selection has brought strategies related to genetic improvement more to the fore across our breed, and we are seeing increased engagement with our R&D programs; building strong Board understanding and support has been critical, expanding our range of collaborative R&D and strengthening our relationships with genotyping providers have been key strategic initiatives
- Minimizing costs of entry to genetic evaluation, in order to encourage participation—and phenotyping—has been an important initiative; and being open to data from a wider range of sources or partners have been important
- Managing the genomic pipeline has been critical, in parallel with faster development of new traits, increasing frequency of evaluations, being actively involved in chip design, and actively initiating R&D (rather than waiting for it to emerge from the R&D community) have all been significant strategic developments for our organization—aiming to lead rather than follow

Breeding Companies:

- We’re now working with multipliers to increase accuracy of data collection for traits that can be recorded in that tier, and investing in new phenotyping, such as individual feed intake
- There has been a redirection of funds internally towards phenotyping, including phenotyping in end-users’ operations; defining our phenotyping strategy—what data to collect, and how to collect it most efficiently, is now central
- Big changes are happening in our breeding program—making much more use of existing phenotypes, and this is stimulating re-defining our breeding direction; the innovation cycle is accelerating

- We're investing heavily in evaluating the technology, but we anticipate significant increase in our investments in phenotyping and genotyping
- Genotyping in the commercial level is being increased, this is changing our relationship with those stakeholders
- Our overall strategy has not changed, but we have identified new R&D

National Evaluation Systems:

- We are seeing increased use of sexed semen since the introduction of genomics, with producers making assigning females to different roles (breeding replacements, or breeding cross-bred progeny) based on their genetic merit
- Genotyping is helping increase engagement across the whole population, as well as bringing new opportunities such as breeding for reduced methane
- Investment in new high-value phenotypes is now clearly part of our R&D strategy, and the partnership with breeds becomes more important
- We are thinking more and more about "where will data come from in the future?", and are becoming more strategically engaged in managing data—what traits, ensuring quality of data
- Data from research projects is now potentially shared with industry, and we are developing new evaluations based on research data
- In the breeding programs where breeders have a role in design, there is heavier use of young males

A number of the observations made in response to this question repeat responses to earlier questions, and so it is possible to draw out some consistent messages, at two levels:

- firstly, relating to elements of the response equation

$$R = i \cdot r_{IT} \cdot \sigma(T) / L$$

where:

R is response to selection

i is standardized selection differentia

r_{IT} is the correlation between the index on which selection is based on the breeding objective

T is the breeding objective

L is the generation interval

Changes in accuracy are typically the first effect of implementing genomic selection, and such changes increase the ratio r_{IT}/L . r_{IT} is accuracy itself, but L changes (reduces, at least potentially) because individuals can be evaluated earlier in life

Changes in accuracy also impact the direction of selection—which is captured by $r_{IT} \cdot \sigma(T)$ —via increases in accuracy for previously hard-to-measure traits—observed as an opportunity to "re-balance" selection and genetic change.

Together, these changes underpin the opportunity to increase both the rate of genetic change and its value.

- Secondly, relating to overall strategy, a number of themes are clear:
 - phenotyping becomes a central concern: what traits to collect data on, how to collect the data (i.e., what individuals, what equipment, what data sources), and how to fund the phenotyping effort.
 - What opportunities are most significant for an individual organization to some extent depends on their pre-existing breeding program design. In broad terms, the first opportunity grasped seems to be to make more use of younger individuals, followed by the opportunity to re-balance selection.
 - All organisations had participated in, or initiated, an R&D phase aimed predominantly at validation—discovering how genomics works and what actual changes are seen. However, importantly, this phase seems to have been relatively short, at least as purely for validation: quite rapidly, new genotyping

and phenotyping effort becomes simply building genomic reference data, and in most cases, expanding the traits being recorded. Extending this point, the organisations had essentially moved to having a continuing “R&D core” in their operations.

- This last point in turn connects with further strategic changes: funding the phenotyping becomes a core business challenge, including to what extent organisations draw on or partner with industry or government funding; and, new data sources and hence potentially new business relationships are considered. This is most obvious in initiatives to capture more data from outside the breeding nucleus (for example, making use of data collected in the multiplier or even commercial tiers), and formalizing contractual relationships to support this.
 - A number of the organizations interviewed were beginning to evaluate opportunities to increase scale of leveraging from the nucleus—mainly via changed involvement with multipliers, exploiting the ease and in some cases lower cost of genomic evaluation.
 - A number of organisations reported use of approaches to managing inbreeding via some form of implementation of Optimal Contributions theory, and several stressed that such was an essential component of implementation of genomic selection. Reflecting the more precise knowledge of relationships available using genomic information, such information can inform design of the sampling for reference phenotyping and genotyping, and the mating design used in the nucleus [Mark Henryon, Anders Vernesen, Klara Verbyla, Brian Kinghorn—pers. comm.].
- Finally, while this was not a direct question, it was clear that in some instances, implementation of genomic selection benefited from and also stimulated synergies with other areas of R&D. A familiar example (to the author) is the interaction between meat science and genetics in the Australian sheepmeat industry R&D—meat science assisted with identification and definition of priority traits to collect phenotypes on, genetic analyses underpinned by genomic information shed new light on variation and co-variation in different aspects of meat quality and eating quality, and the joint focus helped raise industry awareness of opportunities for wide-scale change in product quality and offerings at the consumer level [26]. It seems likely that such synergies will grow—the need to capture the most useful phenotypes to enable appropriately balanced selection, will stimulate new interactions, with the growing interest in emissions reduction and in disease resistance being obvious areas for such interactions [22].

The last observation based on the interviews, responses, and insights, is that all these organisations seemed energized and stimulated by the involvement in implementation of genomic selection: they were getting new insights into what is possible, new ways of thinking about all aspects of their operations, new relationships and partnerships, and a very real sense of excitement at the prospect of faster and more valuable genetic progress.

What about impact?

No questions were asked in any interview about economic evaluation, and no attempt is made here to either review or estimate economic impacts. Ex-ante studies exist, e.g., [27], but a telling indicator of confidence in impact, or at least in success, is that all interviewees were increasing investment in phenotyping, and usually in genotyping, and in increasing scale (of the breeding program and/or commercial production) too. Faster genetic improvement with more comprehensively defined breeding goals should by definition deliver increased value from breeding programs. Analyses of economic impact, at least for programs involving any industry or public funding, can be expected in the coming years.

What about numerically smaller breeds, or less affluent industries or countries?

All the organisations interviewed here are operating in wealthy countries, and as has been reported, usually with some level of industry and/or government investment

in at least R&D stages of the implementation of genomic selection. In addition, they either operate in industries based on large populations of animals (or plants), or have built such populations themselves through commercial growth (as an example, the US Angus breeding sector evaluates over 600,000 new animals per year, providing bulls to a commercial sector of several million animals [Kelli Retallick and Steve Miller, pers comm.].

Scale—both financial and numerical—is important because:

- Phenotyping and genotyping, to generate and maintain the genomic reference population, cost money
- One of the attractions of genomic selection is that such evaluation effort can be focused on a relatively small number of individuals per year (there is no precise formulation to define the number, but around 1–2000 new individuals recorded and genotyped per year will provide a strong basis for selection)

If either funds are extremely limited, and/or the total population is not much larger than the number needed to build a useful genomic reference, possible responses include:

- Organizing the breeding program to exploit the additional accuracy generated by knowledge of the genomic relationships, and aim to grow commercial scale based on faster and more valuable genetic progress. This requires a level of “whole population” coordination, to generate maximum value from the program
- Developing medium- or longer-term investment relationships with government and/or benevolent investors—drawing on justification from the scale and distribution of benefits that would not otherwise accrue to the wider farming population.

These challenges and possible responses are not in fact unique to the implementation of genomic selection—they apply equally to use of any breeding program where performance recording is required (i.e., all breeding programs). What is different is that genomic selection makes more obvious both the investment required and the significance of capturing returns at commercial scale to leverage that investment. Marshall et al. [28] provide some examples of implementation of genomic selection in African livestock, and comment on these challenges.

Wider implications—speculations

The focus of this paper has been on how organisations have implemented genomic selection and what they have learned and changed in doing so. At the same time, it is clear from the responses that the organisations are not intending to return to “pre-genomics”—if anything, as noted above, there is likely to be growth in scale of operation. This can reasonably be interpreted as reflecting increased effectiveness in genetic improvement, and indeed, a number of the interviewees reported quantified increases in rate and value of progress.

Even allowing that this sample of organisations are among lead users of genetic improvement technologies and methods, there seems no reason to doubt that genomic selection will be increasingly implemented to enhance existing genetic improvement schemes across species and countries, notwithstanding that it involves increased, or at least re-directed, investment and the requirement for systems to handle genomic data. What might this mean for R&D generally, and for agriculture more broadly?

Regarding R&D, the point made above about synergies with other disciplines can be generalized: the core R&D activity of genomic selection is the measurement of large numbers of individuals for traits of interest, with experimental design embedded via the combination of knowledge of relationships (via pedigree, whether genomic or not) and of fixed effects (such as location, time, prevailing conditions etc). Genomic reference populations also need to be maintained or refreshed through time, with new phenotyping. Therefore, genomic reference populations provide an excellent platform for diverse research:

- They are by design reflective of the genetic variation in the population of interest, and so any finding is “validated” for that population, and for the medium-term future (in comparison with doing experiments on samples that reflect current commercial generations but previous genetic generations)

- Adding treatments—comparisons of diet or drug regime, for example—can be done in a balanced manner, at whatever scale is affordable, which effectively leverages the overhead costs of the program across more R&D outcomes
- Additionally, by automatically including both a “genetic” and a “non-genetic” dimension, they assist researchers and industry to better appreciate the joint influence of these two dimensions on what can be achieved in terms of performance, including obviously the extent of any genetics-by-environment and/or genetics-by-management interactions.

More generally, the acceleration of genetic progress under genomic selection will inevitably stimulate growth of thinking in two dimensions:

- Firstly, industry and the broader community will come to see genetic improvement as a more powerful, or more precisely rapid, means of change than has been generally appreciated. Despite the fact that changes under selection have been dramatic over periods of one or more decades, e.g., [29], and can mean continuous productivity or profitability improvement that more than matches the cost-price squeeze [30], genetic improvement is still widely spoken of as slow and steady, with the note that it is cumulative added as a generally misunderstood “add-on”. However, when the facts of what can be achieved become more widely appreciated, there seems no reason that focus will not increasingly be paid to how much to invest in phenotyping, which is the fuel of genomic selection. The transformation of dairy breeding—completely reversing previous trends for fertility, the impact of selection for disease resistance in several species [22], and the dramatic increase in scale already apparent in some industries [Matt McDonagh, pers. comm.], signal a technology with rapid, immediate and valuable effect.
- A specific example is the appreciation that genetic improvement can contribute to reduced emissions in agriculture, and can do so without requiring a permanent treatment cost (of some mitigant) at the animal level [31].
- Secondly, the appreciation that essentially any problem can be tackled provided appropriate phenotyping is in place, coupled with the “naturalness” of change via genomic selection, could significantly improve confidence that challenges of sustainable food production with minimal undesirable side-effects can be overcome. This will stimulate more thinking about the true, or complete, breeding goals—expanding beyond simply producing more of the main product(s) to much more “holistic” goals incorporating product, product quality, reduction in disease, reduced environmental footprint, etc. [32], consistent with the more comprehensive approach to valuing changes that has been labelled “Doughnut Economics” [33].

Rational optimism about what can be done to produce more food (and other animal and plant products), of higher quality and health-supporting standard, with less environmental impact can make a real contribution to humanity actually tackling these challenges with a sense of hope.

4. Conclusions

Genomic selection has been implemented in an increasing number of situations since it was first described, building on continuing research into genotyping tools, traits, and methods of utilizing genomic information in breeding. The growing implementation provides practical support for or validation of the benefits proposed for the technology, which centre around opportunity for faster genetic progress, particularly in traits previously difficult to improve (the “hard-to-measure” traits).

The organisations interviewed here reflect a diversity of species, country, scale and position and role within a market economy. Differences are reported in the path to implementation—mainly in rapidity of adoption (in dairy for example, transition to genomic selection was almost instant in some countries) and in the process of evaluation, whether private, public or a mixture.

Despite this diversity, the interviewees report successful implementation in a range of situations, including increased accuracy of estimates of genetic merit, increased rates of genetic progress, and/or growing adoption. At the same time, a number made clear that such changes were not solely due to implementation of genomic selection, the implementation being simultaneous with other R&D and/or extension activities, which contributed to the changes. Where pre-existing breeding program design was advanced, implementation of genomic selection did accelerate progress, essentially making better use of and adjusting the existing breeding program design.

Other themes that emerge, and which reflect opportunities available essentially anywhere, include:

- Increased accuracy of selection (noted above) and the ability to re-balance selection, both contribute to the opportunity to make genetic progress more valuable—both in terms of speed but also in economic value of each unit of change. (In terms of the response equation, this simply means that either i/L and/or $riT.\sigma T$ can be increased, the first ratio expressing speed of change, and the second more the direction and value of change).
- New challenges emerge, or become more obvious:
 - definition of breeding goals becomes even more important both because genomic selection offers the “opportunity” to move faster in the wrong direction, and at the same time offers scope to improve traits previously intractable to selection
 - investment in phenotyping becomes more obviously the underlying rate-limiting parameter, in turn highlighting any challenges in return on investment for breeders or other stakeholders, and potentially requiring new investment relationships, particularly in extensive, multi-stakeholder industries
- Synergies with other disciplines: genomic selection leverages data, and so the more data that is relevant to income and cost in the species production system the better—meaning that drawing on knowledge of a range of disciplines will almost invariably increase value creation.
- The significance of the observation that genomic selection decouples recording from selection takes time to be appreciated, but is profound. As that appreciation grows, the opportunities in terms of both what can be changed through genetic improvement, and the rate at which those traits can be changed, are very clearly re-energising and engender a sense of excitement about opportunities. Genetic improvement can be seen more and more clearly as a “design” enterprise [34], design in the sense of being able to think expansively about what changes are possible.

Overall, the success of implementation, coupled with the appreciation of the scope for genetic improvement, and the recognition that genomic selection is technically benign—it simply increases the effectiveness of the “breed the best to the best” approach which has underpinned agriculture for millennia, together generate a more positive outlook on agriculture—much can be done to make the best and most valuable use of scarce resources, and can be done with much more effective consideration of direct and indirect consequences (direct and correlated responses), as long as we think carefully about what changes we want to make.

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Conflicts of Interest: The author declares no conflict of interest.

Appendix A

The fee schedule for the Council of Dairy Cattle Breeding can be accessed at <https://redmine.uscdcb.com/attachments/download/13496/CDCB-Fee-Schedule-Update-06-22-2021.pdf> (accessed on 20 April 2022).

In the context of this paper, the important point to note is that fees are adjusted for persons or organisations supplying defined phenotypic data on animals.

Appendix B

The individuals interviewed for this paper, and the relevant web links are here grouped as in the body of the paper.

Breeders

Ian Locke, Wirruna Poll Herefords	https://wirruna.com/
Tom Gubbins, Te Mania Angus	https://www.temaniaangus.com/
Lucinda Corrigan, Rennylea Angus	https://www.rennylea.com.au/
Alf Collins, CBV Brahmans	https://cbv.com.au/
Mark Mortimer, CentrePlus Merinos	https://www.centreplus.com.au/
Tom Bull, Lambpro	https://www.lambpro.com.au/
John Keiller, Cashmore-Oaklea	https://www.cashmoreoaklea.com.au/

Breed Associations:

Andrew Byrne and Peter Parnell, Angus Australia	https://www.angusaustralia.com.au/
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Kelli Retallick and Steve Miller (now AGBU), Angus Genetics Inc.	https://www.angus.org/agi
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Matt McDonagh, Australian Wagyu Association	https://www.wagyu.org.au/
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Breeding Companies or Projects:

Anders Vernesen and Mark Henryon, Danish Agriculture and Food Council—re Danbred	https://danbred.com/about-us/
Pieter Knap, PIC	https://www.pic.com/
Matthew Cleveland, ABS Global	https://www.absglobal.com/
Lewis Rands, Peter Kube and Klara Verbyla, re SALTAS	https://tassalgroupp.com.au/our-planet/our-operations/
Rachel Hawken, Cobb-Vantress	https://www.cobb-vantress.com/
Tony McRae, Tree Breeding Australia	http://www.treebreeding.com/
Wallace Cowling, Faba bean breeding	https://research.aciar.gov.au/rapidcookingbeans/news/brio-news-release

National evaluation centres and organisations:

Andrew Cromie, Irish Cattle Breeding Federation	https://www.icbf.com/
Laurent Journaux, INRAE and IDELE—now GenEval	https://www.geneval.fr/english
Hamish Chandler, Meat and Livestock Australia	www.mla.com.au
Joao Durr, Council on Dairy Cattle Breeding	https://www.uscdcb.com/
Mark Thallman, USDA Meat Animal Research Center	U.S. Meat Animal Research Center: USDA ARS
Matt Shaffer, DataGene	https://datagene.com.au/

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