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Strategies and tools for genetic selection in dairy cattle and their application to improving animal welfare

1 **Strategies and tools for genetic selection in dairy cattle and their application to improving animal**

2 **welfare**

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9

10 **Abstract**

11 Genetic improvement of farm animals, especially selection within breeds focussed on high

12 production and efficiency, is often cited as a potential threat to animal welfare. However, many

13 animal welfare issues can be addressed, at least partially, by animal breeding and genetics. In this

14 chapter we explore the relationship between genetic selection and animal welfare, the strategies

15 and tools for genetic improvement and how they can contribute to improved animal welfare. A

16 growing public awareness of animal welfare and environmental issues has led to breeding goals

17 being broadened beyond farmer profitability. As animal welfare and behaviour are complex and

18 multi-factorial, so the emergence of selection indices that include a large number of traits to

19 optimise animal welfare in a way that is consistent with enterprise sustainability for the farmer are

20 necessary.   This trend is likely to continue and will be aided by the advent of new technologies for

21 measuring animal welfare in conjunction with DNA-based predictions of genetic merit (genomic

22 selection). The dairy cattle industry has been a 'poster-child' for the application of genomic

23 selection, in addition to enabling selection decisions to be made earlier in life, it can be used to

24 select for traits that it was not possible to select for previously. These include important welfare-

25 related traits, such as improved disease resistance and heat tolerance. Dairy cattle breeding is a very

26 international activity with just a few breeding companies dominating the market in semen for the

27 most numerous breeds, especially the Holstein. Consequently, genetic diversity within breeds is

28 diminishing and although genetic gain has been spectacular, the rate of inbreeding now presents

29 itself as a threat to the future success of breeding programmes. A greater emphasis on diversity in

30 breeding programmes and the traits under selection are needed as major themes in research and

31 application. Innovation in methods to measure these new traits, (e.g. molecular phenotyping, sensor

32   development, digitalisation data science etc.), could dramatically transform selection for animal

33   welfare, as these technologies can enable large-scale objective measurements of animal behaviours.

34   In addition to animal-based outcome measures, factors like housing, feeding, specific management

35   practises pose other risks to welfare. Risk factors and their interactions have an impact on the

36   development of diseases or other challenges to welfare. Collaborative efforts between animal

37   behaviour scientists, geneticists, engineers, data scientists and others will potentially provide

38   solutions to these challenges.

39

40

41   **Introduction**

42   The study of welfare is focused on improving the lives of animals (von Keyserlingk and Weary, 2017)

43   and encompasses the health and functional fitness of animals in addition to promoting positive

44   psychological states. Consideration of animal welfare is an important part of designing breeding

45   programmes for ethical and commercial reasons; it is clearly important to animals themselves, to

46   farmers and to many consumers, and needs to be considered in designing programmes that are

47   resilient and forward-looking. The three main challenges in designing welfare-friendly breeding

48   programmes are: 1) defining what to improve (referred to as breeding goals by animal breeders) and

49   the welfare indicators to use (referred to as selection criteria by animal breeders); 2) accessing

50   measurements on large numbers of animals in a cost-effective way that can be used for genetic

51   selection purposes to reduce the risks and 3) developing and validating approaches to assess

52   emotional states (Weary et al., 2017) with breeding programmes in mind.

53   Directives such as the OIE (World Organisation for Animal Health) Terrestrial Animal Code

54   (https://www.oie.int/en/what-we-do/standards/codes-and-manuals/terrestrial-code-online-

55   access/) that aims to implement improvement of standards of worldwide animal health and welfare

56   from a veterinary point of view, have highlighted the importance of genetic selection for animal

57   welfare; for example "individual animals within a breed should be selected to propagate offspring

58   that exhibit traits beneficial to animal health and welfare by promoting robustness and longevity.

59   These include resistance to infectious and production related diseases, ease of calving, fertility, body

60   condition score and temperament." Breeding activities facilitate long-term permanent and

61   cumulative improvement of welfare, whereas improved management is faster in the short term, but

62   might not be sustainable or permanent.

63   While selection between breeds and crossbreeding are likely to have impacts on animal welfare, the

64   focus of this chapter is mainly to consider within-breed options including: 1) essential principles of

65   genetic selection; 2) the expansion of dairy cattle breeding objectives to include traits associated

66   with animal welfare; 3) animal welfare in breeding decisions including how technological advances

67   and collaboration are key components of success in this area. The aim of this chapter is to provide

68   examples of where breeding solutions have been applied in the past and thoughts on where this

69   approach might be especially useful in the future, rather than cataloguing an exhaustive list of

70   examples of potential animal welfare solutions applied to the field of animal breeding.

71

72   **Glossary Box (after Simm *et al*., 2021)**

73   Additive genetic effects – the influence on an animal's genotype or phenotype due to genes that act
74   together in a relatively linear and cumulative manner. Estimated breeding values (EBVs) are used to
75   estimate the aggregate effect of such genes on traits of interest.

76   AI or Artificial insemination - deposition of semen into the reproductive tract of a female animal-
77   usually after earlier semen collection, dilution, freezing and storage and subsequent thawing. Allows
78   elite males to produce many more offspring than by natural mating.

79   Breeding goal - the set of traits which a breeding programme is intended to improve.

80   Breeding programme – the set of activities associated with breeding future generations of animals,
81   including choice of breeding objective and selection criteria, recording, genotyping and genetic
82   evaluation of animals, selection and mating of animals, monitoring genetic gain and inbreeding etc.

83   BLUP: Best linear unbiased prediction - statistical procedure for estimating breeding values. Is
84   applied under several sets of assumptions or models which account for different relationships
85   between animals. BLUP estimates environmental effects and breeding values simultaneously, often
86   for multiple traits, and so disentangles genetics from management, feeding etc. more effectively,
87   and leads to more accurate estimates of breeding value than other methods.

88   EBV: estimated breeding value – an estimate of the additive genetic merit of an animal, derived from
89   performance records from the animal itself and/or its relatives, and their pedigree relationships;
90   increasingly also uses genomic information.

91   Genome association studies – establish relationships between genotypes and animal performance in
92   traits of interest; once such associations have been established, this information can be used in so-
93   called genomic selection to identify other animals with the most favourable combination of genetic
94   markers.

95   Genomic selection - selection of breeding animals based on the use of genome-wide genetic markers
96   (usually SNPs) to estimate breeding values. The relationships among genetic marker genotypes and
97   animal phenotypes are first measured in a 'reference population', in order to estimate breeding
98   values of selection candidates from genotypes only or a combination of genotypes and performance
99   records.

100   Genotype – the set of genes/alleles that an animal inherits – may refer to a pair of alleles at a
101   specific locus/site in the genome, or to the collective effect of many loci affecting a trait of interest.

102 Heritability – that fraction of the total phenotypic variation that is due to additive genetic variation;
103 the proportion of superiority of parents that gets passed on to offspring.

104 Heterosis/hybrid vigour – the advantage in performance of crossbred animals over the mid-parent
105 mean for the trait of interest.

106 Introgression – introduction of a new gene of interest (e.g. for polledness), usually via crossing with
107 another breed carrying that gene, followed by backcrossing to the original breed while ensuring
108 breeding animals carry the gene of interest. Some such changes are now possible via gene editing,
109 though this is largely still at an experimental stage.

110 Multi-trait - refers to simultaneous estimation of genetic parameters or breeding values for multiple
111 traits, or simultaneous selection for multiple traits.

112 Non-additive genetic effects – the influence on an animal's genotype or phenotype due to genes
113 that act non-additively e.g. show dominance, where the presence of a dominant allele partially or
114 completely masks the effect of a recessive allele at the same locus; or epistasis, where the effects of
115 a gene at one locus are influenced by the genotype at another locus.

116 Phenotype – is an observable or measurable trait such as stature, milk volume, temperament. The
117 phenotype is a result of the animal's genotype and its 'environment' (essentially all non-genetic
118 influences). The relative importance of these is measured by the heritability.

119 Qualitative traits - traits usually under the control of single genes (e.g. coat colour, polledness, many
120 genetic disorders) that fall into discrete classes.

121 Quantitative traits – traits affected by genes at many different loci (polygenic), as well as by non-
122 genetic factors like feeding and management (often termed 'environmental' effects). The
123 performance of animals in quantitative traits tends to show continuous variation.

124 Selection criteria (auxiliary traits) – the set of measurements on which selection is based; these may
125 be the same as breeding goal traits, where these can be measured directly in candidates for
126 selection, or proxies for these traits.

127 Selection index or total merit index - An overall score of genetic merit allowing optimal selection for
128 multiple traits – with the emphasis on each breeding goal trait usually depending on its relative
129 economic value and the scope for genetic improvement (which depends on the additive genetic
130 variance in that trait and covariance with other traits under selection). Index scores can be derived
131 directly from (multitrait) BLUP EBVs for breeding goal traits and their economic values. Examples
132 include £PLI in the UK and Balanced Performance Index in Australia.

133 SNP – single nucleotide polymorphisms are commonly used genetic markers and are found along the
134 genome where there is variation between individual animals in which of four nucleotide bases (A, C,
135 G and T) are present. Single Nucleotide Polymorphism (SNP) 'chips' are available for most domestic
136 species, that allow detection of variants at 10s-100s of thousands of SNP loci dispersed across the
137 genome.

138 Trait - an animal characteristic of interest in breeding programmes that can be classified or
139 measured and subjected to selection.

140 Threshold model (TM) – a type of statistical model used in the estimation of genetic parameters and
141 breeding values for traits that are influenced by many genes but that have a limited number of
142 categories, and an underlying normal distribution of liability e.g. presence or absence of disease, or a
143 small number of scores indicating severity of disease or degree of calving difficulty.

144

The principles of genetic selection

In this section we outline some of the key concepts and strategies in livestock breeding relevant to dairy cattle welfare. For a fuller description see Simm et al. (2021). Traditionally, there have been three main strategies for the genetic improvement of farmed livestock: (i) selection between breeds or strains, (ii) selection within breeds or strains and (iii) crossbreeding. Newer molecular genetic tools are beginning to augment these strategies, potentially allowing the transfer of genes within or between species (though this has proved more complex in livestock than in crops, and is tightly regulated in most countries), enhancing existing selection approaches via 'genomic selection' (now in widespread commercial use), and allowing the base sequence of genes to be altered in a targeted manner via gene editing (still largely at an experimental stage in livestock, and also subject to tight regulation in most countries). The principles behind each of these strategies and how they can be implemented to improved welfare will be discussed below.

Selection between breeds or stains. For genetic improvement strategies to be effective, it is important to decide what the important traits are (the 'breeding goal'). Historically, scientists and breeders have focussed on traits with the highest economic importance (e.g. milk yield and milk composition), though dairy farmers have long been concerned with the functional fitness of cows, often assessed via the proxy of conformation or 'type' scoring. There is a growing need to consider other traits related to animal welfare and environmental impact that may not be properly recognised by their economic values alone. It is logical to choose the most appropriate breed or cross, based on its performance in this set of traits. Selection between breeds or strains can achieve dramatic and rapid 'one off' genetic change when there are large genetic differences between populations. Further improvement depends on selection within the chosen breed or strain.

Crossbreeding involves mating animals of different breeds, lines or species, for a range of reasons including: (i) improving system efficiency by crossing 'complementary' breeds that excel in different traits – for instance crossing of *Bos taurus* breeds selected for high production with *Bos indicus* breeds showing high heat and disease tolerance in the tropics; (ii) 'grading up' to a new breed or strain – as has happened often over the last few decades in the dairy sectors of many countries; (iv) as an intermediate step in the creation of a new synthetic or composite breed; (vi) to introduce a single gene for a favourable characteristic, such as polledness - the absence of horns - to an existing breed ('introgression'), or (vii) to exploit heterosis or hybrid vigour - the advantage in performance above the mid-parent mean often seen in crosses, and widely applied in some pastoral dairy industries such as that in New Zealand (Lopez-Villalobos et al., 2000).

179

180 Selection within breeds involves comparing animals of that breed and identifying preferred animals

181 to become parents of the next generation. When repeated each generation, this produces

182 cumulative changes in successive generations, as seen in the dairy sector of many countries.

183

184 ***Genetic variation*** There are many traits of interest in farmed animals under the control of single

185 genes (e.g. coat colour, polledness, many genetic disorders). These are often termed qualitative

186 traits, if they fall into discrete classes. Many other traits of interest in animals are affected by genes

187 at many different loci (polygenic), as well as by non-genetic factors like feeding and management

188 (often termed 'environmental' effects). Although classical Mendelian segregation is at work at each

189 of these loci, it is difficult to distinguish different phenotypes. Instead, the performance of animals

190 tends to show continuous variation. Often the performance of animals follows a normal distribution,

191 and is measured on some scale, hence these are termed quantitative traits.

192

193 For quantitative traits it is useful to think of an animal's phenotype being comprised of its genotype

194 (which can be further subdivided into an additive genetic component, or 'breeding value', and a non-

195 additive genetic component) and an environmental component. Modern methods of livestock

196 improvement attempt to disentangle these components as far as possible through the application of

197 statistical methods such as linear models, best linear unbiased prediction (BLUP) etc. (see glossary).

198 Selection between and within breeds acts largely on additive genetic merit, while crossbreeding may

199 be used to benefit from additive or non-additive genetic differences between animals, or both of

200 these.

201

202 Many of the 'tools' used in within-breed selection rest on properties of this normal distribution of

203 performance. For example, the variance in performance in a group of animals can be split into

204 additive genetic, non-additive genetic and environmental components. This allows comparisons of

205 the relative importance of these different sources of variation, and is useful when deciding on a

206 strategy for genetic improvement, and for predicting responses to selection. An important related

207 measure is the heritability of the trait - defined as the ratio of additive genetic variation to total

208 phenotypic variation in the trait of interest. Put simply, it tells us the relative influence of genetics

209 (nature) and environment (nurture) on traits of interest. The profitability and public acceptability of

210 livestock enterprises depends on an increasing number of animal characteristics, and it is important

211 to know how these are related. Phenotypic or genetic correlations (derived from variances and

212 covariances) are used to quantify the association between observed performance or breeding
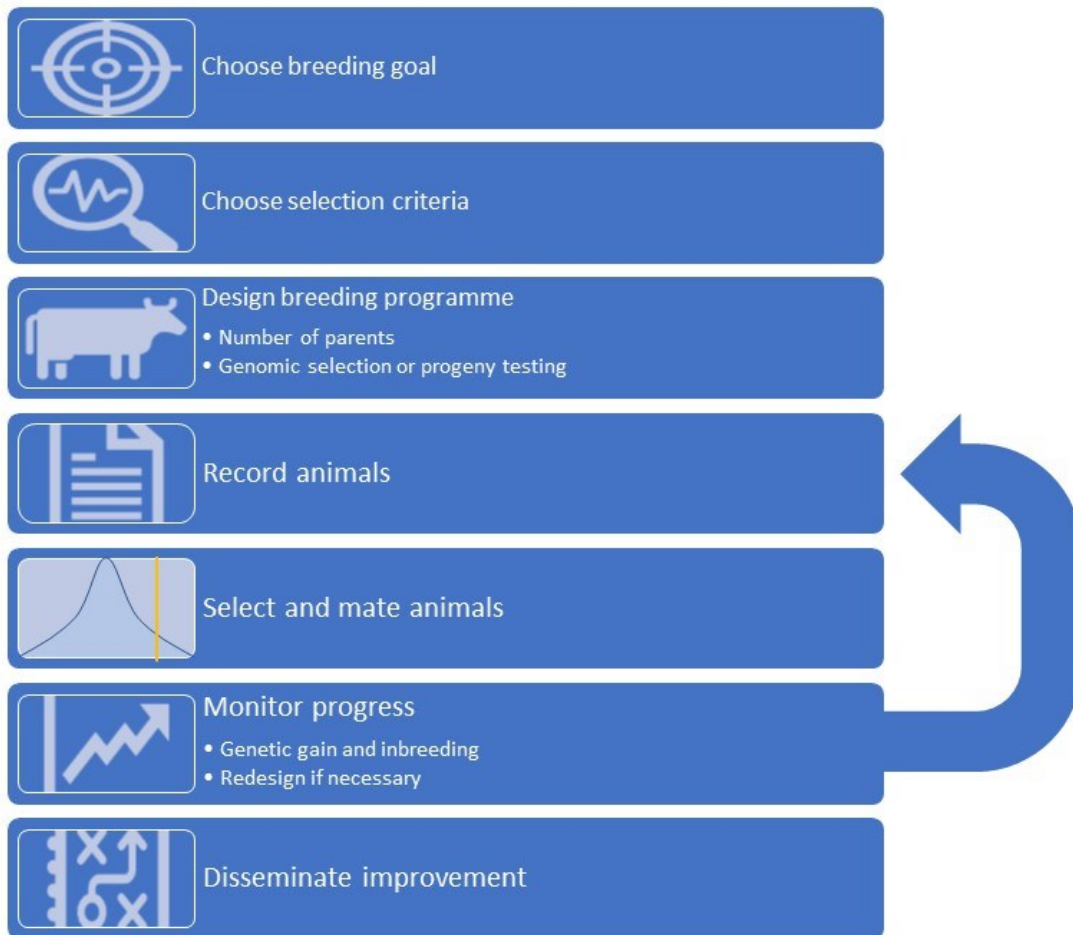
213   values, respectively, in pairs of traits. It is worth mentioning here the special case, relevant to

214   selection for some welfare-related traits, especially disease traits, where we record the presence or

215   absence of disease, or a limited number of categories of severity, rather than the continuous scale

216   we see in many other traits, but there is an underlying normal distribution of 'liability'. These traits

217   require a particular type of statistical model known as a 'threshold model' to derive genetic

218   parameters and estimate breeding values, but respond to selection in just the same way.

219

220   ***Breeding programmes.*** Effective selection within breeds increases the average level of additive

221   genetic merit or breeding value of the population in the traits concerned. The key steps in a breeding

222   programme are shown in Figure 1 and include: (i) defining the breeding goal (the set of traits we

223   wish to improve); (ii) deriving relative economic values for breeding goal traits – this helps optimize

224   the weighting on different traits in a multi-trait selection index; (iii) deciding on the selection

225   criterion (the traits we measure on candidates for selection - these may be breeding goal traits

226   themselves, or proxies for these, e.g. if breeding goal traits cannot be measured directly because

227   they are expensive, expressed in one sex only, or expressed late in life); (iv) estimating 'genetic

228   parameters' for the breeding goal traits and selection criteria – especially the phenotypic and

229   genetic variances for key traits and the covariances among them, and the heritabilities and

230   correlations derived from these (co)variances; (v) designing the breeding programme e.g. deciding

231   on the numbers of males and females to be selected annually, to achieve a balance between

232   maximizing genetic gain and minimizing levels of inbreeding; (vi) implementing the programme i.e.

233   doing the routine recording, genetic evaluation (estimating breeding values of candidates for

234   selection) and mating of animals; and (vii) monitoring progress and redesigning the programme

235   where necessary e.g. if there are unforeseen consequences of selection, or markets change.

236

237   *Figure 1. Steps involved in within breed improvement programmes based on objective performance*

238   *(after Harris et al. (1984); Simm et al. (2021)).*

Choose breeding goal

Choose selection criteria

Design breeding programme
- Number of parents
- Genomic selection or progeny testing

Record animals

Select and mate animals

Monitor progress
- Genetic gain and inbreeding
- Redesign if necessary

Disseminate improvement

239

240

241   For many traits that are associated with animal welfare (e.g. disease resistance, calving ease,

242   thermal comfort), while the heritability is low (i.e. genetic variation is proportionately small when

243   compared to the non-genetic variation) the genetic variation that exists may still be relatively high in

244   absolute terms (meaning that there are large genetic differences between some individuals and

245   families). On top of this, selection of farm animals can only be effective when the traits of interest –

246   or alternative selection criteria, or correlated traits – are measurable and accurately recorded. A

247   further complication is that, even within a herd, animals do not necessarily face an equal disease

248   challenge, so interpretation of disease records is complex (Bishop and Woolliams, 2010). In addition

249   to error, other non-genetic sources of variation include feeding, climate, chance events and other

250   unknown effects and these may dominate the measurable variation of many traits. Together, these

251   often contribute to low heritability estimates for many animal health and welfare traits.

252

253   ***Genetic and genomic evaluations***. Estimated breeding values (EBVs) are used to identify the best

254   candidates for breeding. Best linear unbiased prediction (BLUP) is a very widely used statistical

255 technique that disentangles genetic from environmental effects in the best possible way, and so

256 produces the most accurate EBVs. Conventionally, BLUP uses performance records from related

257 animals to increase the accuracy of EBVs. The more records, and the closer the relationships of

258 recorded animals to the target animal, the more accurate the EBVs. Until recently, most dairy cattle

259 breeding programmes have been based on structured progeny testing of young AI bulls, with

260 daughters' performance for a wide range of traits being recorded in commercial herds. Very

261 accurate EBVs can be produced for bulls with many hundreds of daughters recorded. In the last

262 decade or so, the practice of genomic selection has virtually supplanted planned progeny testing in

263 many industrialized countries – we discuss this later. Typically, breeding values for dairy cattle are

264 estimated nationally by genetic evaluation units that are often part of government ministries, breed

265 societies, universities or research institutes. For many years INTERBULL – a subcommittee of the

266 International Committee for Animal Recording (ICAR) – has provided guidance on, and helped

267 harmonize approaches to, genetic evaluation, as well as providing international evaluations that

268 combine information optimally from multiple countries.

269

270 A range of molecular genetic tools is enhancing our ability to select for desired performance or

271 inherited disease status. Increasingly, automated methods are available for detecting genetic

272 polymorphisms (variations in the bases present at particular sites on the chromosome – these

273 variations exist within coding regions of genes, but also in many other parts of the genome). Single

274 Nucleotide Polymorphism (SNP) 'chips' are available for most domestic species, that allow detection

275 of variants at 10s-100s of thousands of SNP loci dispersed across the genome. This in turn allows

276 whole genome association studies, where particular sequences of SNPs identify segments of the

277 genome associated with a trait e.g. high milk yield, or disease resistance. Once such associations

278 have been established, SNP information can be used in so-called genomic selection to identify other

279 animals with this favourable combination of SNPs (see Figure 2). This allows earlier estimation of

280 breeding values (as genotypes can be obtained directly on candidates for selection much sooner

281 than performance records), higher accuracy of EBVs (especially when genomic and performance

282 records are combined), or both. Within the last decade, breeding programmes have changed from

283 using progeny testing to genomic selection in many countries, where the best bulls mated to the

284 best females are young bulls selected based on their genomic EBV. Genomic selection has

285 transformed livestock breeding internationally because, in addition to enabling selection decisions to

286 be made earlier in life, genomic selection can be used to select for traits that were not accessible

287 before, including important welfare traits, such as improved disease resistance, resilience to climate

288 variability and thermal stress etc.

289

Figure 2. Genomic prediction using a reference population of known phenotypes and genotypes is used to generate a genomic prediction equation which is applied to genotyped animals. The best animals are selected for breeding using the genomic breeding values derived from this equation. (Adapted from Goddard and Hayes (2009), (Eggen, 2012))
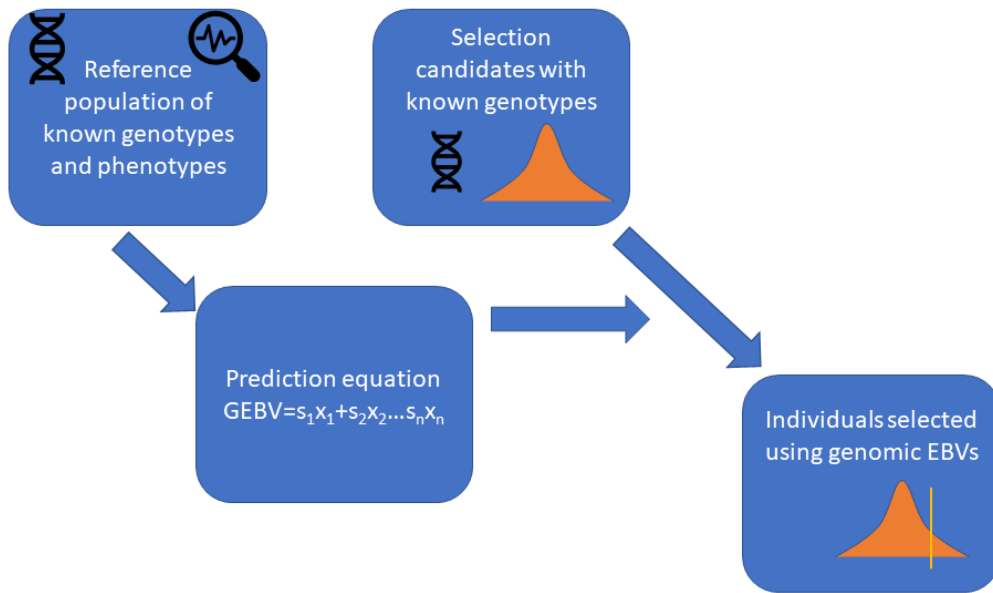
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Rates of genetic gain. Annual rates of response to selection in polygenic traits depend on four main factors: (i) the selection intensity achieved (i.e. the superiority of selected parents above the mean), (ii) the accuracy with which genetic merit in the trait of interest is predicted (accuracy of estimating breeding values), (iii) the amount of additive genetic variation in the trait of interest, and (iv) the generation interval (the average age of parents when their offspring are born). Generally speaking, the higher the selection intensity, accuracy and genetic variation, and the lower the generation interval, the higher the annual rate of genetic improvement. Breeders have most control over the selection intensity and generation interval (but both within biological limits) and – at least at a national level - choice of method to estimate breeding values.

Rates of genetic gain in production traits, fertility, longevity and udder health have increased substantially since the introduction of genomic selection; largely driven by reduced generation intervals (García-Ruiz et al., 2016). Dedicated female reference populations that have entire herds of genotyped cows with these measurements recorded are a valuable source of information for these new traits. In addition to national genetic evaluation units, commercial companies are also developing their own genomic predictions for health traits through use of health data collected on cows that are genotyped.

Livestock breeding industries in industrialized nations often have a pyramid structure, with elite or nucleus breeders at the top, one or more middle tiers of purebred or crossbred multipliers, and a final tier of commercial herds or flocks, or end users. Pig, poultry and dairy cattle breeding operations in many countries are dominated by a relatively small number of international breeding companies who supply breeding stock to commercial producers. Because of the widespread use of artificial insemination (AI) in dairy cattle breeding, breeding companies supply semen from elite dairy bulls, with most elite cows owned by individual farmers. AI also allows commercial dairy farmers to directly access elite genetic material, bypassing the multiplier tiers present in other sectors.

Genetic improvement, including selection between breeds, crossing and within-breed selection has led to dramatic changes in the performance of dairy cattle over the last 70 years or so (Simm *et al*., 2021). The development and widespread adoption of technologies for semen collection, freezing and artificial insemination (AI) in dairy cattle has both enabled effective genetic improvement in many countries through progeny testing, and – together with related embryo transfer technologies –

333 led to international exchange of genetic material, and dairy cattle breeding becoming a truly

334 international endeavour.

335 Genetic selection in domesticated species has been practiced with a great deal of success and has

336 focussed primarily on improving traits that have market value or are associated with reducing costs

337 of production. For example, Cole and VanRaden (2018) showed around 300kg increase in fat yield

338 for US Holstein cows born from 1957-2015. From the 200kg/yr base in 1957, genetics and

339 management/feeding each representing 28% of the gain. A major challenge now is to extend this

340 approach to characteristics, like those associated with animal welfare and environmental impact of

341 livestock, that have high societal value but low or hidden current market value.

342 **Including animal welfare in dairy cattle breeding objectives**

343 Animal welfare is an area of science that generally includes the measurement of multiple indicators

344 to assess the physical, behavioural and emotional state of the individual (Broom, 1991). Some of

345 these states are difficult to quantify or measure objectively. Animal breeding on the other hand

346 relies on objective measurements, although breeding values are often developed as a by-product of

347 data primarily collected for farm management decisions. For example, milk production breeding

348 values are generally estimated using pedigree data, genomic data and data collected from routine

349 milk-recording. Fertility breeding values use mating and pregnancy test data either recorded by

350 farmers or professional service providers; health breeding values largely use clinically recorded data

351 (as diagnosed by veterinarians or farmers), while longevity EBVs use data on herd-entry and exit

352 dates. Other examples include claw health recorded by professional hoof trimmers, conformation

353 scoring, auction sales, slaughterhouse data, etc. There are many other examples of breeding values

354 that are by-products of recording for another purpose. Egger-Danner et al. (2015) describe the

355 potential sources of data and their uses. Typically, a genetic evaluation unit will produce a set of >30

356 breeding values for different traits.

357 *Single-trait selection*. For many years, selection focused on milk production traits and conformation

358 in many countries. Conformation, or the appearance of cows has for a long time been regarded by

359 producers as helping to ensure that their cattle are productive and long-lasting, in addition to taking

360 honours in the show-ring or pedigree sales (Miglior et al., 2017). In the late 1990s, it became clear

361 that an undesirable consequence of narrow, production-orientated selection criteria was a reduction

362 in health and fertility. The decline in fertility, in particular, has been well documented (Lucy, 2001,

363 Berry et al., 2014). But, there was also evidence that there were unfavourable genetic correlations

364 between production traits and other animal welfare traits, (e.g. mastitis resistance, lameness,

365 reproductive and metabolic disorders), which were starting to deteriorate (Rauw et al., 1998). This

366   led to a large number of studies focused on determining the extent of genetic control of health

367   traits, generally through the use of clinical observations of disease. The heritability estimates from

368   these studies show that generally the genetic control is small (Table 1), yet there is sufficient genetic

369   variation to make genetic progress.

370   ***Selecting for health traits***. Before the consequences of narrow dairy breeding objectives described

371   above were widely understood, the Nordic countries already had a long history of recording and

372   providing genetic evaluations of health traits. For example, in Norway, veterinary treatments had to

373   be registered on an individual basis from 1975 (Heringstad and Østerås, 2013), with similar schemes

374   being established in Denmark, Finland and Sweden through the 1980s. In addition to the Nordic

375   countries, routine genetic evaluations of mastitis have been in place in Austria and Germany since

376   2010, and in France and Canada from 2012 (Egger-Danner et al., 2015), with many others following.

377   Valuable lessons that have been learnt by dairy geneticists and others about the dangers of narrow

378   breeding goals. In addition to selection on fertility, disease resistance traits have become key areas

379   where breeding values are being developed for future breeding goals.

380

381   **Table 1**. Ranges of heritability estimates of udder health, lameness and claw disorders and metabolic

382   diseases summarised from 3 recent review papers

	Model	Range in heritability estimate	Review paper
Udder health			Egger-Danner et al (2015)
Clinical mastitis		0.02-0.09	
Improved SCC		0.01-0.17	
Electrical conductivity		0.12-0.36	
Pathogen information		0.04-0.09	
Lameness and claw disorders			Heringstad, Egger-Danner et al. (2018)
Digital dermatitis/interdigital dermatitis	LM	0.01-0.11	
	TM	0.09-0.20	
Heel horn erosion	LM	0.03-0.07	
	TM	0.09	
Interdigital hyperplasia	LM	0.01-0.14	

	TM	0.19-0.39	
Sole haemorrhage	LM	0.02-0.08	
	TM	0.07-0.09	
Sole ulcer	LM	0.01-0.12	
	TM	0.07-0.18	
White line disease	LM	0.01-0.09	
	TM	0.06-0.10	
Lameness	LM	0.02-0.10	
	TM	0.02-0.15	
Locomotion	LM	0.03-0.11	
Metabolic diseases			Pryce et al. (2016)
Ketosis	LM	0.01-0.08	
	TM	0.02-0.16	
Milk fever	LM	0.01-0.08	
	TM	0.09-0.18	
Displaced abomasum	LM	0-0.08	
	TM	0.12-0.32	
Tetany	LM	0.004	
	TM	0.02-0.05	

383

384　Out of all the diseases common in dairy cows, lameness is considered to be a key welfare indicator

385　(Table 2) with feet and leg problems being common. For example (Van der Waaij et al., 2005)

386　estimating that 70% of cows in the Netherlands have at least one hoof issue. Pain associated with

387　injury or disease of feet or legs is often manifested by lameness and inhibits behaviours such as time

388　spent feeding, rumination, altering lying behaviour etc (Whay and Shearer, 2017). Although

389　management and housing play a key part in controlling lameness, genetic improvement is a strategy

390　worthy of consideration. Genetic improvement of hoof health can be achieved through data collected

391　from hoof trimming, veterinary treatments or on-farm databases. Lameness scoring can be used as in

392　auxiliary trait for prediction of claw health (Heringstad and Egger-Danner et al. 2018).

393　Another promising approach is to develop breeding values for different types of lameness, as there

394　is evidence to suggest that heritabilities vary between claw diseases recorded by hoof trimmers

395　(Ødegård et al., 2013, Buch et al., 2011). This requires the development of preferably national

396　databases of accurate and consistent data records. In fact, there has been a lot of effort recently to

397 harmonize recording of claw disorder e.g. the ICAR claw health atlas; (Egger-Danner et al., 2014).

398 The increase in electronic capture of data has enabled the assembly of much more in the way of

399 clinical observations of disease, with many farmers keeping electronic records as evidence for

400 quality assurance programmes.

401 *Predictor traits*. Many traits that are currently evaluated are correlated, so selection for one

402 breeding value can have favourable (or unfavourable) effects on other traits. Perhaps the best

403 example of this is selection for mastitis resistance using somatic cell count. Many countries first

404 introduced mastitis EBVs through a proxy trait of somatic cell count (SCC), which can be considered

405 to be the cow's immune response to infection. When SCC is high, the cow is responding to a likely

406 infection in the udder. Since then including farm or veterinary records on mastitis observations has

407 become more prominent in the development of breeding values for mastitis.

408 Heringstad et al. (2006) showed that selection against mastitis leads to favourable correlated

409 responses to selection in other diseases, such as ketosis and retained placenta, indicating the

410 existence of a general robustness or reduced liability to disease. Selecting for general disease

411 resistance, or immunity is also becoming popular. For example, in a study by De la Paz (2008)

412 comparing cows with high and low antibody and cell-mediated immune response, high responders

413 had a decreased risk of disease occurrence for several diseases, including mastitis, ketosis, metritis

414 and retained placenta. The heritability of response to an immunity challenge is high enough to justify

415 selection (Thompson-Crispi et al., 2012). In fact, selection tools for immunity are available

416 commercially. Semex (www.semex.com) sells semen from bulls identified as being high and low

417 antibody and cell-mediated responders to an immune challenge. The high responders were found to

418 have half the disease occurrence compared with low responders (Thompson-Crispi *et al.* 2012).

419 Body condition score (BCS) is often considered to be an indicator of hunger, reduced fertility (Banos

420 et al., 2004), or metabolic disease (Pryce et al., 2016), and therefore a welfare indicator. A survey by

421 the International Committee on Animal Recording on the use of welfare indicators showed that body

422 condition score and lameness were the most popular (Table 2). Body condition score is often part of

423 the suite of conformation traits scored by breed societies, or is part of quality assurance systems and

424 is only recorded once a year and only from a subset of animals in the herd. Thus, evaluating changes

425 that may indicate a change in welfare is not easy. However, BCS is reasonably heritable (Pryce and

426 Harris, 2006) and already considered as part of the breeding objective in countries such as New

427 Zealand (Zhang and Amer, 2021) with the justification that the costs associated are incurred through

428 having to replenish body reserves mobilised in lactation, especially if cows being thinner leads to

429 earlier drying off dates and less days in milk. For more information refer to:

430 https://www.dairynz.co.nz/animal/animal-evaluation/interpreting-the-info/economic-values/

431

432 *Table 2. Top 10 welfare indicators from ICAR survey (adapted from Haskell (2019):*

433 *https://www.icar.org/Documents/Prague-2019/Presentations/02%20-%20Marie%20Haskell.pdf*

Welfare indicator	No. Scoring
Body condition score	28
Lameness in loose-housed cows	24
Diarrhoea	18
Temperament	16
Skin alterations, swellings or injuries	16
Lameness in tie-stalls	16
Existing records	16
Cleanliness	15
Claw trimmer data	13
Hampered respiration	11

434

435 **Resilience**. An area of growing interest is resilience, which could have positive implications for

436 animal welfare. Resilience is defined as "the capacity of an animal to be minimally affected by

437 disturbances, or to rapidly return to the state pertained before exposure to a disturbance" (Colditz

438 and Hine, 2016). A disturbance can be physical (disease, temperature) or emotional (e.g. negative

439 interaction with humans, novel environments, social stressors) (Berghof et al., 2019). In terms of

440 animal welfare, it is likely that an animal with better resilience will have a less negative experience

441 during the disturbance than one with lower resilience.

442 This area of research has led to novel ways to calculate traits of interest, for example the variance of

443 a trait under a particular challenge may describe the impact of a disturbance on individuals in a

444 population, so the animals with least variation may be more resilient to their environment than the

445 others (Berghof *et al.,* 2020). Using daily milk yields from automatic milking systems (AMS), Elgersma

446 et al. (2018) showed that cows with low within-cow variation in milk yield had genetically less

447 disease and greater longevity. Following on from this, Poppe et al. (2021) proposed that AMS can be

448 used to identify cows that have low within-cow variability in milk yield (deviations from the expected

449   lactation curve) and fast recovery after a challenge event, and that these are likely to be the most

450   resilient.

451   Another example of a measure of resilience is the reduction in yield (i.e. slope) after passing a

452   temperature and humidity index (THI) threshold (Figure 2). Cows that are more tolerant to heat have

453   less steep slopes (i.e. a smaller reduction in production as temperature and humidity rise). Nguyen

454   et al. (2016) used the decline in milk, fat and protein yields as THI increases as indicators of heat

455   stress. The study found that using high density SNP genotypes, heat tolerance genomic breeding

456   values can be predicted at the accuracy of 0.42 – 0.61. Genomically predicted heat susceptible and

457   predicted heat tolerant animals show significantly difference in milk yield losses, rectal and intra-

458   vaginal temperatures when experiencing a mild simulated heat wave (Garner et al., 2016). Clearly,

459   traits associated with resilience is a growing area that could produce new solutions to breeding for

460   improved animal welfare.

461 *Figure 2. Heat tolerance defined as the slope of decline in milk, fat or protein yield when temperature*
462 *and humidity exceed a thermoneutral threshold*

463
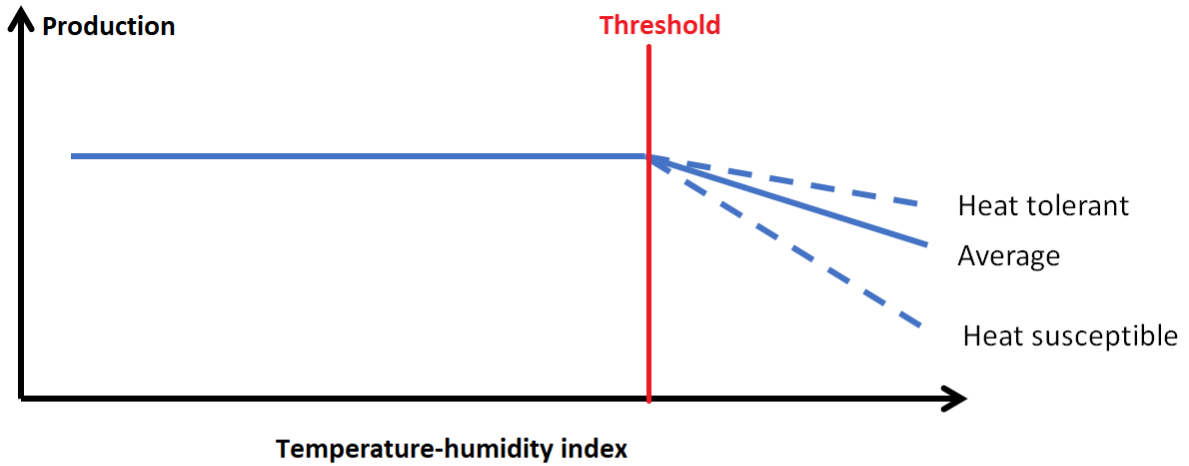
464

465

466 ***Selection indices***. As we have shown, there are now many traits that can and should be included in
467 breeding programmes. Being able to select for many traits simultaneously has led to a considerable
468 amount of work developing multi-trait selection indices, building on the approach developed by
469 Hazel (1943). The idea is that farmers can focus on a single index score when selecting breeding
470 animals, instead of selecting for multiple EBVs simultaneously.

471 A selection index starts with the identification of the breeding goal, which is often net farm profit
472 broadly representing at least the following categories: milk production, type, longevity, udder
473 health, fertility, other traits (Egger-Danner *et al.,* 2015). The breeding goal is calculated as the sum of
474 each EBV multiplied by a weight, which is usually based on the economic or perceived value of the
475 trait. A selection index for n traits can be written as:

476 $$\text{Index} = b_1 EBV_1 + b_2 EBV_2 + b_3 EBV_3 + \ldots + b_m EBV_n,$$
477
478 where the b-values are the weights to each of the EBVs. Selecting on this index gives the highest
479 selection response in genetic merit such as ranking for highest profit.

480

481 ***Selection indices for improved animal welfare***. Currently, animal welfare is rarely considered in

482 deriving the weights to apply to traits in a selection index, with these typically based solely on

483 economic parameters . For example, the cost of disease is generally used to calculate economic

484 values for disease resistance traits. It is challenging to appropriately define the weights from an

485 animal welfare perspective, as it is adding a subjective layer to an objective process (i.e. we need to

486 put a value on the animal's experience of a disease or other welfare issue), as animal welfare is an

487 ethical concept requiring societal input. However, if these challenges can be overcome, then a

488 framework exists to devise non-market values to apply to traits under selection (Nielsen et al.,

489 2005).

490 The thinking to date takes into consideration consumer willingness to pay for aspects of traits that

491 have perceived societal or animal welfare value. It is also possible to devise indices that have either a

492 desired outcome, or selection response, or restrict the change in a trait. Other aspects affecting

493 breeding objectives will some become more important, for example, as the growing human

494 population places more pressure on limited resources and global changes leading to hotter and drier

495 – or otherwise more extreme - conditions in which to manage livestock, there is also a need to

496 recognise increased consumer awareness of animal welfare and farming conditions. So, future

497 breeding goals need to adapt to these considerations by including economic, societal and

498 environmental considerations simultaneously (Boichard and Brochard, 2012, Martin-Collado et al.,

499 2015).

500 An approach that has gained some traction in existing breeding programmes is placing additional

501 emphasis on traits perceived to be associated with improved animal welfare. Martin-Collado et al.

502 (2015) used the "1000 minds" methodology to add objectivity to perceived non-market values

503 through a survey, where questions on perceived values are assessed through a series of comparisons

504 that are of similar actual value. The idea being that if opinions are canvassed from many farmers

505 (hence the "1000 minds" name), then the comparative value of a trait to groups of farmers with

506 similar philosophies can be quantified. This approach was the foundation to determine farmer

507 preferences for national selection indices being developed in Australia. Although farmer preferences

508 were the focus of the research by Martin-Collado et al. (2015), it was clear that animal welfare and

509 improving the functional ability of dairy cows was at the forefront of farmers' desires for future

510 generations of cattle, with 3 traits associated with health ranked in the top 5. To provide selection

511 tools that give farmers of different philosophies an index that best suited their needs 3 indices were

512 released for Australian dairy breeders in 2015 to use in selection decisions (Byrne et al., 2016). At

513 around the same time the total merit index (TMI) used for selecting Fleckvieh and Brown Swiss cattle

514   in Austria and Germany was updated to include farmer preferences (Fuerst-Waltl et al., 2016). In

515   this process more emphasis was placed on fitness traits.

516   Indices or sub-indices that focus entirely on animal welfare traits may start to emerge, especially as a

517   vehicle to capture the complexity of animal welfare. For example, if we want to achieve favourable

518   selection responses in psychological state in addition to health and productivity, then the first task is

519   to identify selection criteria. While the health and productivity part of our breeding objective may

520   have an economic dimension, and therefore be at least partially captured in our current selection

521   indices, the positive psychological response is much more challenging and is only starting to emerge

522   as a potential selection criterion.

523   **Other considerations**

524   ***The interaction with environment.*** An animal's performance is a result of the genes it inherits and the

525   environment in which it is kept, including climatic factors and a host of management factors. Livestock

526   keepers have long been aware of the fact that some breeds or strains perform better in some

527   environments than others – termed a genotype x environment (GxE) interaction. There is good

528   evidence, for instance, that *Bos taurus* dairy breeds highly selected for production in temperate

529   climates often perform worse (e.g. lower production, higher disease incidence, shorter herdlife) than

530   tropically-adapted *Bos indicus* breeds, or crosses with these, in tropical environments with extreme

531   thermal, nutritional and disease challenges (see Simm *et al.,* 2021). GxE interactions also lead to

532   differences in the ranking of sires within a breed, in different production systems (Figure 3). Hence, it

533   is crucially important for animal welfare that appropriate breeds or crosses are chosen for particular

534   environments and systems when GxE interactions are present. Evidence to inform such decisions may

535   come from experimental studies or analysis of industry data.

536

537   *Figure 3. Change in relative performance of two animal breeds or crosses across low, medium and high*

538   *challenge environments.*

539   *Animal A performs better than animal B in low and medium challenge environments, in higher challenge environments the*

540   *performance of A and B deteriorate and cross over (re-rank), so that B performs best in the highest challenge*

Scaling G x E   Re-ranking G x E

Phenotypic performance

A

B

B

A

Low   Medium   High

Environmental challenge
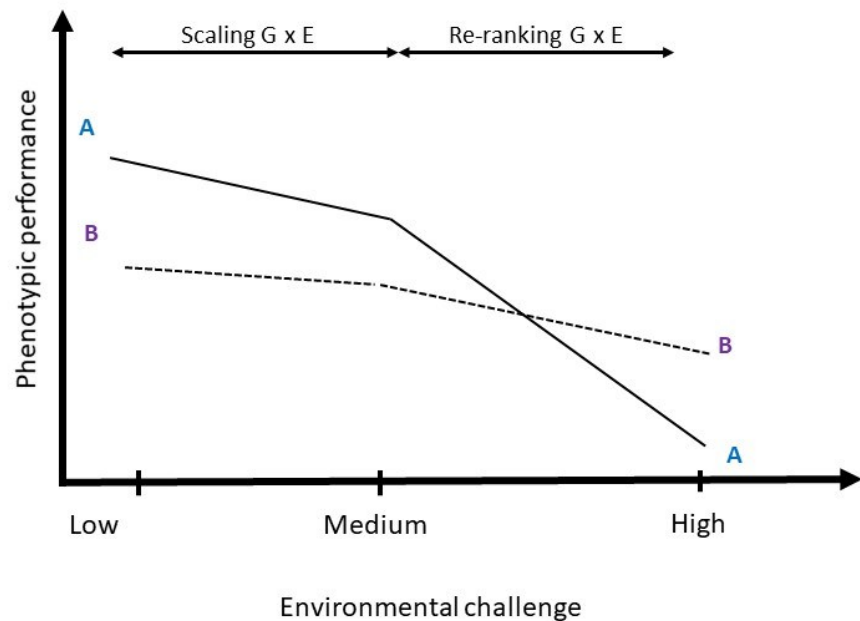
541

542

543   Although risk factors such as stocking density, stall size, etc. pose direct issues for animal welfare, it is

544   how animals deal with these risk factors that often has a genetic component. Moreover, there is

545   reason to believe that substantial GxE interactions exist i.e. that the ranking of sires or families for

546   welfare indicators differs between environments at the herd level. To date, most GxE studies have

547   explored interactions between countries. However, Zwald et al. (2003) found that the heritabilities of

548   production traits in colder climates within the USA were lower than in hot climates (0.26 and 0.39,

549   respectively), and the genetic correlation between these two groups was 0.66, implying that heat

550   stress may play a role in genotype by environment interactions. Understanding of the interaction

551   between genetics and the environment needs to grow, in order for researchers to attempt to predict

552   performance or risk in different systems. The use of machine learning methods i.e. learning from

553   patterns in data, lends itself disentangling this information and enabling predictions of risk (Lasser et

554   al., 2021) which should partly help to improve management across systems/environments.

555

556   *Inbreeding*. Although conserving genetic diversity is not itself a welfare concern, the consequences

557   of it are. Inbreeding arises when the parents of an individual are genetically related. More

558   specifically it is close to zero when there are no common ancestors and increases if the parents are

559   closely related. The consensus is that inbreeding depression is the result of the 'load' of deleterious

560   recessive genes arising from common ancestors. Fitness traits such as fertility (McParland et al.,

561   2007) and health (Baes et al., 2019) are especially sensitive to inbreeding. Inbreeding also leads to

562   the manifestation of genetic diseases (arising from single deleterious mutations). Inbreeding is

563   especially important in dairy cattle because AI and genomic selection allow very intense selection of

564   males, and AI facilitates rapid international dissemination of genes from favoured sires. Moreover,

565   the concentration of breeding decisions in a few global companies in a highly competitive market

566   arguably leads to a focus on shorter term marketability rather than longer term sustainable use of

567   genetic variation.

568   The downside to accelerating rate of genetic gain (largely through genomic selection) has been the

569   impact it has had on effective population size, especially in popular dairy breeds, such as the

570   Holstein (Makanjuola et al., 2020). Effective population size is a measure that accounts for the

571   number of breeding males and females in a population, not just the overall population size and

572   current estimates are 43-66 in the Holstein breed (Makanjuola et al., 2020). This provides a better

573   indicator of genetic variability in a population, and changes in this over time. There has been an

574   increase in the rate of inbreeding reported in most dairy populations (VanRaden et al., 2011,

575   Makanjuola et al., 2020) with evidence that the rate of inbreeding has accelerated since the

576   introduction of genomic selection (Doublet et al., 2019). Conserving diversity and genetic variation is

577   important to maintain dairy genetic resources and reduce the consequences of inbreeding, such as

578   inbreeding depression in fitness traits.

579   As inbreeding increases, the risk of homozygous deleterious recessive mutations existing also

580   increases. A mutation is a change in the nucleotide sequence of the genome and most are harmless

581   and rare, and some are positive - in fact mutations give rise to genetic variation. With the

582   widespread international use of selected sires via AI, heterozygote 'carriers' of such recessive genes

583   can spread quickly in the population before affected homozygous descendants appear and are

584   detected. There are examples of genetic diseases that arise as single mutations, such as Complex

585   Vertebral Malformation (CVM), Bovine Leucocyte Adhesion Deficiency (BLAD) and Deficiency of

586   Uridine Monophosphate Synthase (DUMPS) in Holsteins. Most of these diseases are the result of

587   reasonably recent (rare) mutations. For example, complex vertebral malformation, or CVM, can be

588   traced to two former elite Holstein sires. Because of their widespread use, the sires appeared on

589   both sides of the pedigree of affected calves (Agerholm et al., 2001). More recently, a mutation

590   affecting calf survival has been identified and is associated with cholesterol deficiency leading to

591   emaciated calves that fail to thrive and presents a serious animal welfare issue (Kipp et al., 2016). At

592   its peak, 13% of registered Canadian Holsteins calves were affected. The occurrence of these

593   diseases highlights the importance of managing rates of inbreeding, which arises as a result of the
594   co-occurrence of common ancestor(s).

595   Genomic data can be used to control or monitor inbreeding in a population by quantifying genomic
596   relationships between animals in addition to estimating inbreeding depression (Baes et al., 2019,
597   Bjelland et al., 2013). One of the advantages in using genomic, rather than pedigree relationships, is
598   that it is a more accurate estimate of identity by descent, because it does not suffer from lack of
599   depth of pedigree data and pedigree errors. The use of genomic metrics should allow breeders to
600   improve management of the risks associated with inbreeding, allowing better evaluation of the
601   trade-offs between the genetic value of the progeny and the undesirable side effects
602   associated with inbreeding (Baes et al., 2019).

603

604   **New technologies, traits and methods**

605   The way an animal interacts with its environment affects its welfare and detrimental responses
606   could loosely be described as negative experiences or "stress". Brito et al. (2020) described how
607   aspects of the hypothalamic-pituitary-adrenal (HPA) and sympathetic-adrenal-medullary (SAM)
608   systems have genetic variation and could be useful targets. For example, glucocorticoid
609   concentrations (cortisol and corticosterone) may be indicative of stress (König and May, 2019). An
610   alternative approach is to consider behavioural traits instead. For example, in their review Haskell *et*
611   *al.* (2014) cited 4 studies where cortisol was higher in excitable animals than calm animals, with the
612   measurable behaviour being temperament. A 'good' temperament in the dairying context is often
613   described as a calm response to being milked and docility at handling (Haskell et al., 2014).
614   Temperament is often included in genetic evaluations and is evaluated using farmer recorded scores
615   on a scale such as 1-5 and could become a trait for consideration in more welfare-focused selection
616   indices.

617   *Sensors.* Emerging technologies are likely to facilitate the development of breeding values for
618   behaviours. These could include cameras, microphones (for vocalisations), body temperature
619   sensors, or accelerometers (Brito *et al.,* 2020). For example, wearable sensors using accelerometers
620   can provide massive quantities of longitudinal data that can help in defining traits associated with
621   cow comfort, such as the amount of time spent ruminating, lying, feeding, walking etc (Bikker et al.,
622   2014). One of the advantages of embracing sensor defined phenotypes, is that they can be used to
623   detect the risk of disease, or compromises in animal welfare, before clinical disease has occurred.
624   While this is clearly advantageous for management purposes, it could be argued that the primary

625 objective of a health breeding value is to select against the occurrence of clinical cases. So, although

626 sensor data are likely to become a valuable addition to estimating breeding values into the future,

627 especially as a way to collect very large amounts of objective data, sensor data could also be used to

628 record clinical manifestations of disease.

629 From a technical perspective, incorporating data from multiple sources is a well-established process

630 in animal breeding through the implementation of multi-trait models. One advantage of sensor

631 systems or cameras is that they can provide continuous measurements. Development of EBVs using

632 this potentially massive source of data is largely in its infancy (Cole et al., 2020) and there are still

633 many hurdles to overcome, including differences between systems, lack of uniformity across devices

634 and lack of integration with national databases leading to disconnected data silos (Lasser et al.,

635 2021). So, to date, the contribution of sensor data to EBVs is under-explored.

636 ***Mid-infrared spectroscopy.*** One of the most promising ways of evaluating sub-clinical disease is the

637 mid-infrared (MIR) analysis of milk samples. MIR is used routinely to quantify the fat, protein, casein,

638 lactose and urea concentration of milk in milk-recording programs. Many farmers participate in

639 these programs as they use the data for management decisions. So again, the MIR data is a by-

640 product of an alternative use of these data. MIR analysis of milk has been used to predict other milk

641 characteristics such as fatty acid composition, milk protein composition, milk coagulation properties,

642 milk acidity, mineral composition and ketone bodies (De Marchi et al., 2014). Recently (Luke et al.,

643 2019b) showed that biomarkers of early lactation disease (measured in serum) are predictable using

644 MIR analysis. Furthermore, many of these biomarkers are also heritable and show promise for

645 genomic selection (Luke et al., 2019a, van den Berg et al., 2021). It seems likely that as we gain

646 further understanding of the potential value of these measurements, breeding of dairy cattle will be

647 further transformed.

648

649 ***Gene editing***. Gene editing allows genetic material to be added, removed or altered at specific

650 locations on the genome. Gene editing is especially useful for traits where a small number of edits

651 are required. Two examples of how this technology can be used to improve animal and human

652 welfare is in selecting for hornless (polled) cattle or breeding cows that are tolerant to heat stress.

653 Successful inclusion of the polled allele into dairy breeds would eliminate horns in dairy cattle

654 (Mueller et al., 2019). Most dairy heifers are disbudded or dehorned at an early age and although it

655 is a standard management practice, without the use of appropriate anaesthetics and analgesics it

656 can be very painful and it is increasingly scrutinised by the public as a potential welfare issue. In *Bos*

657 *taurus* breeds polledness is controlled at a single locus, with the polled allele dominant to the

658 horned allele. Therefore, mating a homozygous polled bull (PP) to a herd of horned cows (hh) will

659 result in all the offspring being polled (Ph). If a bull is heterozygous (Ph) and the cows are horned

660 (hh), then half the offspring will be polled (Ph). Two mutations that prevent development of horns in

661 certain breeds of cattle have been mapped on the bovine genome (Medugorac et al., 2012) and

662 these have become targets for gene editing (Fahrenkrug and Carlson, 2014).

663 The so-called 'slick' mutation is also a target for gene-editing. The slick mutation is an adaptation to

664 heat found naturally in Senepol cattle, where it appears to be associated with the type of coat, being

665 slick or smooth, with some possible alteration to sweating ability (Davis et al., 2017). Breeding

666 programs in some countries including Puerto Rico and the USA have already started incorporating

667 the slick mutation in Holstein cattle without the use of gene editing (Carabaño et al., 2019); (Hansen,

668 2020), which will enable the use of the desirable mutation with little to no background genetics from

669 the donor breed.

670 Gene editing has the potential to be used in a more extensive way to provide a combination of

671 desirable characteristics such as thermotolerance, disease resistance and polledness, although the

672 successful editing of large numbers of alleles at different loci has not been reported yet (Van

673 Eenennaam, 2019), but could become a reality. However, gene editing could largely complement

674 traditional breeding techniques and programmes (Van Eenennaam, 2019).

675

676 **Putting it all together**

677 To make the most of these opportunities, expertise from many different disciplines is required. We

678 need think-tanks of animal scientists and technologists to think collaboratively on measurements

679 that could be useful for genetic evaluation purposes. For example, to capture animal welfare

680 adequately in breeding programmes we need to include measurements that capture an animal's

681 emotional state in addition to physical state. It is likely that some of the technologies we have

682 discussed will lend themselves to capturing some of this information, however, working with

683 engineers and data scientists to generate records of the welfare indicators we wish to measure is a

684 priority area for the future. One approach is to first test and validate these measurements in

685 research herds and then take the most promising to more numerous genotyped populations to

686 develop genomic prediction equations that can be used to select individuals. Finally, we need to

687 understand the genetic correlations between these new selection criteria and the traits we currently

688 select for. Providing the new measurements pass these stages, the final step is taking the

689 measurements and genotypes to genetic evaluations. This can be either public (i.e. for all farmers to

690 use), or for proprietary marketing by large independent breeding companies and then marketed
691 exclusively on their bulls.

692 Financial incentives or penalties on the basis of genetic merit for welfare associated characteristics,
693 such as inbreeding metrics, could also be considered with checking using genotyping. If these
694 approaches are useful, they could even complement, or to some extent replace farm audits. There
695 are also opportunities for supermarkets to insist on their suppliers having welfare focused breeding
696 programmes.

697 **Concluding statements**

698 Dairy cattle breeding has a mixed past with regard to animal welfare. Narrow breeding goals that
699 focused almost entirely on milk production traits have been detrimental to many animal traits
700 associated with welfare. Increasing awareness of welfare issues and the broadening of breeding
701 goals to include animal welfare traits are welcome changes. Advances in understanding the genetics
702 of welfare-related traits, and technologies and methodologies for recording and evaluation of these
703 can help prevent welfare problems and allow active pursuit of better welfare. Collaborative efforts
704 between animal behaviour scientists, geneticists, engineers, data scientists and others will
705 potentially provide solutions to these challenges.

706

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