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## Breeding the dairy cow of the future – what do we need?

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24 **Abstract**

25 Genetics is responsible for approximately half the observed changes in animal performance in well-  
26 structured breeding programs. Key characteristics of the dairy cow of the future include 1) produce a  
27 large quantity of high value output (i.e., milk and meat), 2) good reproductive performance, 3) good  
28 health status, 4) good longevity, 5) does not eat a large quantity of food, 6) easy to manage (i.e., easy  
29 calving, docile), 7) good conformation (over and above reflective of health, reproductive performance  
30 and longevity), 8) low environmental footprint, and 9) resilient to external perturbations. Pertinent and  
31 balanced breeding goals must be developed and implemented to achieve this type of animal;  
32 excluding any characteristic from the breeding goal could be detrimental for genetic gain in this  
33 characteristic. Attributes currently not explicitly considered in most dairy cow breeding objectives  
34 include product quality, feed intake and efficiency, and environmental footprint; animal health is  
35 poorly represented in most breeding objectives. Lessons from the past deterioration in reproductive  
36 performance in the global Holstein population remind us of the consequences of ignoring or failing to  
37 monitor certain animal characteristics. More importantly, however, current knowledge clearly  
38 demonstrates that once unfavourable trends have been identified and the appropriate breeding strategy  
39 implemented, the reversal of genetic trends is achievable, even for low heritability traits like  
40 reproductive performance. Genetic variation exists in all the characteristics described. In the genomics  
41 era, the relevance of heritability statistics for most traits is subdued; the exception is traits not  
42 amenable to routine measurement in large populations. Phenotyping strategies (e.g., more detailed  
43 phenotypes, larger population) will remain a key component of an animal breeding strategy to achieve  
44 the cow of the future as well as providing the necessary tools and information to monitor  
45 performance. The inclusion of genomic information in genetic evaluations is, and will continue, to  
46 improve the accuracy of genetic evaluations which in turn will augment genetic gain; genomics,  
47 however, can also contribute to gains in performance over and above support of increased genetic  
48 gain. Nonetheless, the faster genetic gain and thus reduced ability to purge out unfavourable alleles  
49 necessitates the appropriate breeding goal and breeding scheme and very close monitoring of  
50 performance, in particular for traits not included in the breeding goals. Developments in other  
51 disciplines (e.g., reproductive technologies) coupled with commercial struggle for increased market  
52 share of the breeding industry, imply a possible change in the landscape of dairy cow breeding in the  
53 future.

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55 **Keywords:** Genetics, heritability, genomic, breeding objective

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58 **Introduction**

59 Genetics is responsible for approximately half the observed changes in animal performance in  
60 well-structured breeding programs; change here implies improvements (e.g., milk production) and  
61 deterioration (e.g., reproductive performance). Almost all, if not all, individual characteristics, have a  
62 genetic basis. Once genetic variation exists, then breeding for improvement is possible. Moreover,  
63 despite antagonistic genetic correlations existing among some traits (e.g., milk production and  
64 reproductive performance; Berry et al., 2014b), once the genetic correlations are less than unity, then  
65 genetic improvement in all traits is achievable; whether or not this is an appropriate strategy will be  
66 determined by the relative (economic) importance of the respective traits.

67 Lessons from the past suggest that the definition of a holistic and pertinent breeding goal is of  
68 fundamental importance. Genomic selection (Meuwissen et al., 2001) is receiving considerable  
69 attention of late as a tool to increase genetic gain. If however the most pertinent breeding objective  
70 and associated breeding program is not in place, then genomic selection could actually have serious  
71 repercussions for gains in dairy herd profit. Not all traits included in a breeding objective are  
72 amenable to routine measurement on very large populations from which to estimate breeding values.  
73 Controlled experiments on animals divergent for the breeding goal can be efficiently used to elucidate  
74 the expected correlated responses to selection for difficult/expensive to measure traits. Thus, the first  
75 and most important step in deciding “what do we need” for a successful breeding program is to define  
76 the characteristics of the cow of the future. Once defined, the extent of genetic variation governing  
77 these characteristics and the genetic inter-relationships among these characteristics can be quantified.  
78 The final step is to define the best strategy (i.e., phenotyping, genetic evaluations, exploitation of  
79 genomic information) to achieve the desired gains. Continuous evaluation of the performance of the  
80 breeding strategies, including genetic change in the different traits and the cost:benefit of alternative  
81 breeding strategies, should be routinely undertaken.

82

83 **Characteristics of the ideal cow**

84 When initially defining the ideal cow, it is crucial not to 1) overlook traits despite the  
85 sometimes perceived lack of genetic variation in the trait, and 2) ignore a trait if it cannot be (easily)  
86 measured given the current state-of-the-art. Also, when the objective is to define the ideal cow to  
87 guide a breeding program, the ideal cow should be that of the future. Therefore, traits of likely future  
88 importance and their associated (societal) values (e.g., environmental footprint) as well as the future  
89 production system the cows are likely to be producing in, must be considered.

90 Characteristics of the dairy cow of the future include

- 91 1) Produce a large quantity of high value output (i.e., milk and meat)
- 92 2) Good reproductive performance
- 93 3) Good health status
- 94 4) Good longevity
- 95 5) Does not eat a large quantity of food
- 96 6) Easy to manage (i.e., easy calving, docile)
- 97 7) Good conformation (over and above reflective of health, reproductive performance and
- 98 longevity)
- 99 8) Low environmental footprint
- 100 9) Resilient to external perturbations

101

102 All the aforementioned characteristics cannot be taken in isolation. A cow, for example, that  
103 produces a large quantity of high value output but does not eat a large quantity of food will likely  
104 enter negative energy balance which in turn has unfavourable ramifications for animal health and  
105 reproductive performance (Beam and Butler, 1999; Collard et al., 2000).

106 *Production of a large quantity of high value output.* Almost all international dairy cow  
107 breeding goals include milk, fat and protein yield. Milk fat is composed of both saturated and  
108 unsaturated fats, as well as the respective individual fatty acid components. The correlation, for  
109 example, between total milk fat composition and saturated milk fat composition is 0.90 (Soyeurt et al.,  
110 2007) suggesting some (limited) variability in the saturated content of fat exists. Similarly, milk  
111 protein is composed of a casein and whey fraction as well as the individual protein fractions. Milk  
112 processing characteristics (e.g., milk coagulation properties) are also important determinants of milk  
113 quality, especially in production systems supplying markets of high value added (speciality) cheeses  
114 (Sturaro et al., 2013). Although these individual components currently do not have an explicit  
115 economic value in most production systems, they can influence consumer perception of milk products  
116 and thus market demand. For example, the average milk fat of a dairy cow contains 70% saturated  
117 fatty acids, 25% monounsaturated fatty acids and 5% polyunsaturated fatty acids (Grummer, 1991).  
118 Currently dairy products provide 15% to 25% of the fat consumption in the average human diet but  
119 represents 25 to 35% of the saturated fat intake (Chillard et al., 2001). Interest has also intensified  
120 recently in selection schemes for increased milk lactose yield. The genetic correlation between milk  
121 yield and lactose yield is 0.979 (Miglior et al., 2007) indicating limited (but exploitable) genetic gain  
122 is achievable.

123 Although the main source of revenue from dairy herds is milk, beef, through the sale of cull  
124 cows and surplus calves, represents 10-20% of the gross income in most production systems (van der  
125 Werf et al. 1998). Thus, beef merit, however defined, is an important characteristic of dairy  
126 production and the future dairy cow. The importance of beef characteristics of dairy cows may be

127 greater with the availability of low-cost and effective sexed semen as well as production systems  
128 where herd size is limited (e.g., finite land in grazing dairy production systems).

129 *Good reproductive performance.* The importance of excellent reproductive performance in  
130 dairy production systems has been extensively discussed for both seasonal-calving (Shalloo et al.,  
131 2014) and confinement (Cabrera, 2014) production systems. Parturition is required for lactation and  
132 good reproductive performance is necessary to maximise revenue (e.g., longer lactations in seasonal  
133 calving herds) and reduce costs (e.g., hormonal interventions). The importance of superior  
134 reproductive performance is greatest in seasonal calving herds where the calving season is  
135 synchronised with the availability of low-cost feed (e.g., grazed grass). In seasonal calving herds,  
136 compromised reproduction is synonymous with the necessity for involuntary culling. The observed  
137 decline in reproductive performance in Holstein dairy cows in most populations until the early 2000's  
138 (Berry et al., 2014b) eroded the revenue generated from the concurrent increase in milk production  
139 over the same time period (Evans et al., 2006).

140 *Good health status.* Not only does sub-optimal animal health erode herd profit through  
141 increased medicinal requirements and reduced performance (i.e., yield and reproductive performance)  
142 but compromised animal health status also influences consumer perception of modern-day dairy  
143 production systems. Some health issues also incur explicit financial penalties; milk price, for example,  
144 in most countries is tiered based on the somatic cell count of the herd bulk milk pool. Producers are  
145 predominantly concerned with clinical signs of infection but non-observed, often sub-clinical disease,  
146 also impairs performance (Dohoo and Martin, 1984; de Graaf and Dwinger, 1996). Past experience  
147 from the observed decline in reproductive performance in the global Holstein population (Royal et al.,  
148 2000; Evans et al., 2006, Berry et al., 2014b) clearly indicates that monitoring of temporal trends in a  
149 trait or suite of traits is vital to identify unfavourable trends early.

150 *Good longevity.* A second lactation cow yields approximately 16 to 19% more than a first  
151 lactation cow while a third lactation cow (e.g., mature cow) yields approximately 28 to 31% more  
152 than a first lactation cow (Horan et al., 2005; Walsh et al., 2007). Therefore, achieving good longevity  
153 will not only reduce herd replacement cost but will increase herd revenue through the achievement of  
154 mature herd yield but also greater calf price of surplus calves from older cows (McHugh et al., 2010).  
155 Moreover, younger parity cows are more prone to calving difficulty (Berry et al., 2007; Mee et al.,  
156 2011), stillborn calves (Berry et al., 2007; Mee et al., 2008), and disease (Berry and Meaney, 2005)  
157 thereby impacting both labour requirements and overall herd profit; of course very old cows are also  
158 more prone to some diseases (Roche and Berry, 2006). The impact of reduced replacement rate on  
159 herd genetic gain must also be acknowledged; assuming a rate of genetic gain in calves born of 1%  
160 per annum, a halving of replacement rate from 20% to 10% (assuming culling is independent of

161 genetic merit) equates to a loss in gain of just 0.1% per annum. In addition to the considerable impact  
162 on farm profit, poor cow longevity is also a growing consumer concern.

163 *Does not eat a large quantity of feed.* Feed costs represent 50% to 80% of the overall costs of  
164 production in contrasting dairy production systems (USDA-NASS, 2011; Shalloo et al., 2004).  
165 Reducing feed intake, therefore, without any repercussion on the other animal characteristics  
166 described is likely to reduce costs and thus improve herd profitability. There is increasing  
167 commentary on the use of residual feed intake (RFI) as a measure of efficiency in dairy production  
168 systems (Berry and Crowley, 2013) to reduce feed intake without necessarily impacting other  
169 performance traits. Selection for (lower) RFI or reduced feed intake is sensible within an overall  
170 breeding goal that includes all the aforementioned characteristics. If all the components of statistical  
171 model used to derive RFI are included in the breeding objective, then inclusion of either RFI or feed  
172 intake in the breeding objective is mathematically equivalent. Although a large proportion (0.86;  
173 Coleman et al., 2010) of the feed intake phenotypic variation in lactating dairy cows can be explained  
174 by the energy sinks and other confounding effects (e.g., year), phenotypic variation in RFI  
175 nonetheless exists. Lower feed intake implies lower herd feed costs, but also potentially greater cow  
176 numbers in dairy cow grazing production systems.

177 *Easy to manage.* Expanding herd size, and in some regions, access to only labour with less  
178 expertise in animal husbandry requires an easy-care cow. Characteristics of an easy-care cow not  
179 already accounted for (i.e., good health and fertility) include good animal temperament and no  
180 requirement for assistance at calving. Polledness is also a management trait, as is the ability of the  
181 animal as a new-born calf to be vigorous and ingest and absorb sufficient colostrum. Milking speed  
182 could also be considered as an ease of management trait as it affects milking parlour throughput.  
183 Berry et al. (2013) reported considerable phenotypic variation in milking duration among animals  
184 even after accounting for differences in the associated milk yield (and somatic cell count); the  
185 phenotypic correlation between milk yield and milking duration was 0.48. Berry et al. (2013) reported  
186 a phenotypic standard deviation of 102.2 seconds per milking for milking duration independent of  
187 milk yield; across a 305-day lactation, milked twice daily, this equates to a standard deviation of over  
188 17 hours. Therefore, considerable gains in milking parlour throughput may be achievable with  
189 selection for faster milking speed independent of milk yield and udder health.

190 *Good conformation.* Certain animal morphological characteristics are phenotypically  
191 associated with improved reproductive performance, health (e.g., mastitis, lameness) and longevity  
192 (Berry et al., 2005; Larroque and Ducrocq, 2001). Good udder conformation, however, is required for  
193 efficient automatic milking and the appropriate animal size is necessary for the design of the milking  
194 parlour as well as the housing facilities. Good cow conformation may become more influential on  
195 cow longevity as the actual longevity of dairy cows improve through genetic selection. Therefore,

196 correlations between cow conformation and longevity may become stronger as factors other than  
197 reproductive performance influence the likelihood of culling.

198 *Low environmental footprint.* Animal agriculture generates greenhouse gas emissions (GHG)  
199 as methane (CH<sub>4</sub>) from enteric fermentation and manure, nitrous oxide (N<sub>2</sub>O) from the widespread  
200 use of nitrogenous fertilizers and animal manure, nitrates from animal excretion, and carbon dioxide  
201 (CO<sub>2</sub>) from the fossil fuels for energy usage plus land use change. Methane, however, is not only an  
202 environmental hazard but is also associated with a loss of carbon from the rumen and therefore an  
203 unproductive use of energy (Johnson and Johnson, 1995). O'Mara (2011) stated that animal  
204 agriculture is responsible for 8.0 to 10.8% of global greenhouse gas emissions based on calculations  
205 from the Intergovernmental Panel on Climate Change (IPCC). If however complete lifecycle analysis  
206 (i.e., accounting for the production of inputs to animal agriculture as well as change in land use such  
207 as deforestation) is undertaken this figure can be up to 18%. Cattle are the largest contributors to  
208 global greenhouse gas emissions (O'Mara, 2011).

209 One element of environmental footprint, practically ignored to date in animal production  
210 systems, is the efficiency of water usage. Water is overtaking oil as the world's scarcest critical  
211 natural resource (Solomon, 2010). Although the statistic of a 70% increase in food demand between  
212 the years 2010 and 2050 is often quoted (FAO, 2009), less often quoted is the prediction by the  
213 United Nations (UNEP, 2008) of a 50% increase in global water demand between the years 1995 and  
214 2025. Irrigation currently covers 20% of all cultivated land and is responsible for approximately 40%  
215 of agricultural production (Molden, 2007). Rosegrant et al. (2002) projected that by 2025, 64% of the  
216 world's population will live in water stressed basins, an increase from 38% in 2006. Agriculture is by  
217 far the greatest user of freshwater in the world (Jury and Vaux, 2007; Morison et al., 2008; Passioura  
218 and Angus, 2010) accounting for 70% of total freshwater use (Steinfeld et al., 2006). Therefore low  
219 water requirement as well as low methane emissions may be a desirable characteristic of the cow of  
220 the future.

221 *Resilient to perturbations.* There is considerable commentary on the impact of ruminant  
222 production systems on climate change. Less discussed, however, is the impact of climate change on  
223 ruminant production systems. Climate change is expected to result in rising global temperature,  
224 changes in patterns of precipitation, and more extreme weather events. As well as imposing heat stress  
225 on individual animals, such climatic changes may alter the geographical risk areas for certain diseases  
226 (Yatoo et al., 2012) which may have implications for animal populations naïve to such diseases. The  
227 animal of the future, therefore, as well as achieving all the aforementioned characteristics, will have to  
228 be robust to various external perturbations. Because of the definition of heritability, such perturbations  
229 are likely to have less impact on higher heritability traits estimated from field data.

230

231 **Existence of genetic variation**

232 Most discussions on breeding programs and genetic gain focus on heritability estimates for  
233 different traits. Heritability however is only one of the factors that influences genetic gain. Annual  
234 genetic gain for a given trait may be described as (Rendel and Robertson, 1950):

235 
$$\Delta G = \frac{i \cdot r \cdot \sigma_g}{L}$$

236 where  $\Delta G$  is annual genetic gain;  $i$  is the intensity of selection;  $r$  is the accuracy with which you know  
237 the genetic merit of each animal,  $\sigma$  is the genetic standard deviation, and  $L$  is the generation interval.  
238 The accuracy of selection is affected by both the heritability of the trait and the information available  
239 on the animal itself and its relatives. Heritability summarises the proportion of phenotypic variation,  
240 or differences among a cohort of animals, attributable to genetic variation between individuals.  
241 Animal breeders are generally concerned with the narrow sense heritability ( $h^2$ ), which is the  
242 proportion of phenotypic variation attributed to additive genetic variation (i.e., allelic effects  
243 transmitted from one generation to the next). Heritability varies from 0 (not heritable) to 1 (fully  
244 heritable); heritability estimates for a range of performance traits in dairy cattle are given in Figure 1.  
245 In general, traits associated with viability and fitness (i.e., health and reproductive performance) are  
246 lowly heritable while traits associated with animal morphological characteristics are more highly  
247 heritable corroborating similar observations in other species (Visscher et al., 2008; Falconer and  
248 Mackay, 1996).

249 Figure 2 illustrates the interaction between the number of half-sib progeny records and  
250 heritability on the accuracy of selection (ignoring parental contribution). For a given number of  
251 progeny, the accuracy will be greater for higher heritability traits. Accuracy of selection of near unity  
252 is nonetheless achievable, even for low heritability traits, if sufficient information is available.  
253 Therefore, with the appropriate breeding programme (e.g., large paternal half-sib groups, exploitation  
254 of genomic information) and infrastructure for the collection and storage of data, genetic gain in low  
255 heritability traits is certainly achievable if ample genetic variation is present. Hence, one could argue  
256 that the importance of heritability in the genomics era is less compared to historically when evaluating  
257 the potential of animal breeding to achieve the cow of the future at a population level. What is  
258 important is the extent of genetic variation present. Therefore scientific studies must always report the  
259 genetic variance for the traits being evaluated; this information has not always been provided in  
260 studies heretofore.

261 Figure 1 summarises the coefficient of genetic variation for a range of performance traits in  
262 dairy cattle. The coefficient of (genetic) variation is used because it is unit-less and therefore  
263 facilitates the direct comparison of the variation present in traits differing in mean values but moreso  
264 the units of measurement. Although heritability estimates varies considerably across traits, the



265 coefficient of genetic variation is relatively consistent across traits (~5%). The existence of  
266 considerable genetic variation in all traits clearly signifies that once high accuracy of selection is  
267 achievable, rapid genetic gain in each of these traits is indeed possible. The actual rate of genetic gain  
268 achievable for a trait is a function of the relative (economic) weighting on the trait within the overall  
269 breeding goal but also the genetic correlations between that trait and the other traits in the breeding  
270 goal.

271

## 272 **Derivation of a breeding goal to achieve the ideal cow**

273         Once the desired animal characteristics to be considered in the breeding goal have been  
274 decided, and the existence of genetic variation in these traits demonstrated, the relative importance of  
275 each should be quantified. From a breeding perspective, avoidance of double counting should be  
276 ensured. For example, in a breeding goal that includes milk production and fertility with their  
277 associated relative economic weights, the economic value on health should not include the effect of  
278 compromised health on either production or fertility. This is because an animal genetically  
279 predisposed to compromised health will also, on average, have inferior genetic merit for milk  
280 production and fertility (because of the genetic correlations; Berry et al., 2011a). The economic  
281 repercussions of this association will be captured through the economic values and estimated breeding  
282 values of the animal for milk production and fertility. This is why the economic values on some traits  
283 in breeding goals may appear less than expected.

284         Some traits currently have no explicit economic value (e.g., greenhouse gas emissions) or the  
285 expected responses to selection may not be socially acceptable. For example, the economic values in  
286 the UK national dairy cow breeding goal are such that genetic merit for calving interval is expected to  
287 deteriorate. This is because it is not economically appropriate to suffer a loss in genetic gain in other  
288 performance traits if a greater emphasis is placed on reproductive performance (Berry et al., 2014b).  
289 Several studies have proposed approaches on how to best include such traits in breeding objectives  
290 (Nielsen et al., 2005; Wall et al., 2010). Desired gains selection indexes or restriction selection  
291 indexes (i.e., a form of desired gains index) can be applied to achieve a theoretical gain in these traits.  
292 It must be acknowledged that using such desired gains approaches will reduce the expected gain in  
293 profit (Gibson and Kennedy, 1990) unless the index weighting on the constrained trait in the  
294 unrestricted selection index is zero. Alternative approaches to deriving the relative weights on traits  
295 within a breeding goal include interpretation of results from a Delphi study (or other form of survey)  
296 or PAPRIKA (Potentially All Pairwise RanKings of all possible Alternatives; Hansen and Ombler,  
297 2009). Whatever the approach, the expected responses to selection should be calculated and ideally  
298 these expected responses should be acceptable to stakeholders (e.g., producers, consumers).

299 Concern exists about the impact on overall genetic gain from including (too) many traits in a  
300 breeding goal due to a perceived dilution in emphasis on the “more important traits”. Figure 3  
301 illustrates the expected responses to selection for a given trait based on alternative two-trait breeding  
302 goals relative to a breeding goal with only one trait. An accuracy of selection of 0.99 is assumed for  
303 both traits and the genetic correlation between the traits is altered from -0.5 to +0.5. The genetic  
304 variance times the relative economic value of the second trait was either equal or double that of the  
305 first trait depending on the scenario investigated. It is sometimes (incorrectly) thought that including a  
306 trait in a breeding goal with a zero genetic correlation will not impact genetic gain in the other trait(s).  
307 For example, such a conclusion is often used when discussing RFI since, if derived using genetic  
308 regression, RFI will be independent of the traits included in the regression (i.e., milk production).  
309 Figure 3 illustrates that this is not true since it alters the selection intensity for the other traits in the  
310 breeding goal. This is more clearly demonstrated in Figure 4 where the top 10% of animals on a  
311 combined index includes, some, but not all of the top 10% of animals in each trait thereby reducing  
312 the selection intensity for each trait and thus genetic gain. Therefore, including RFI derived using  
313 genetic regression in a breeding goal will reduce the rate of genetic gain in, for example, milk  
314 production; the extent to which it reduces the genetic gain will be a function of the difference in  
315 genetic variance and relative weighting on both traits.

316 The impact of genetic gain in a given trait is expected to reduce as the number of additional  
317 traits included in the breeding objective increase. The extent of the reduction in genetic gain for the  
318 original trait is dependent on 1) the genetic covariances among the breeding goal traits (reduction is  
319 expected to be larger if negative associations exist and the economic weights are the same sign), 2)  
320 the weighting on the additional traits relative to the original trait (genetic gain in the original trait is  
321 reduced as the relative weight on the additional traits increase), 3) the genetic variance of the  
322 additional traits (genetic gain in the original trait is reduced if the relative genetic variance of the  
323 additional traits is greater) and, 4) the accuracy of the genetic evaluations of the additional traits based  
324 on information on the additional traits themselves (genetic gain in the original trait will be reduced if  
325 the accuracy of the genetic evaluations of the additional traits based on information on those traits  
326 themselves increase). This phenomenon is illustrated in Figure 5 which depicts the relative genetic  
327 gain expected for a given trait as the number of traits included in the breeding goal increases. In this  
328 example the genetic variance and economic values of all traits were assumed equal, zero covariances  
329 were assumed to exist among all traits, and the accuracy of selection for all traits was 0.99. Relative to  
330 a breeding goal with just a single trait, the genetic gain in the original trait is expected to be 22% of  
331 the original gain when an additional 19 traits are included in the breeding goal. If the relative  
332 weighting of all 19 additional traits was just 10% of the original trait, then the expected genetic gain  
333 in the original trait was 91% of the genetic gain expected with a single-trait breeding goal.

334 There is much on-going discussion about if including RFI, with a low associated reliability, in  
 335 a breeding goal will adversely affect genetic gain. A two trait breeding goal including protein yield  
 336 and RFI is assumed with a genetic standard deviation times the relative economic weight on both  
 337 traits being approximately similar (Bell et al., 2013; Gonzalez-Recio et al., 2014); zero genetic  
 338 correlation is assumed between both traits. If the reliability of genetic evaluation for RFI is 10%, the  
 339 genetic gain for protein yield is 96% that of a breeding goal that included only protein yield (although  
 340 RFI is expected to also improve); a reliability of 20% for RFI reduces the genetic gain in protein yield  
 341 to 91% of that achievable with single trait selection for protein yield. Based on the scenarios  
 342 simulated here, although including additional traits in a breeding goal is likely to reduce genetic gain,  
 343 the impact is expected to be less for the more important traits (assuming the genetic variance of all  
 344 traits is the same and zero covariances exist). More importantly, inclusion of the additional  
 345 (important) traits in the breeding goal will increase the overall response to selection on the entire  
 346 breeding goal (Figure 5).

347 The relative emphasis on an individual trait  $i$  in a breeding goal is usually depicted as the  
 348 product of the genetic standard deviation times the economic weight of that trait divided by the sum of  
 349 the same calculation for all traits in the breeding goal:

350 
$$\text{Emphasis}_i = \frac{|a_i \cdot \sigma_i|}{\sum_{j=1}^n |a_j \cdot \sigma_j|} .$$

351 where  $a_i$  and  $a_j$  is the economic value for trait  $i$  and  $j$ , respectively and  $\sigma_i$  and  $\sigma_j$  is the genetic standard  
 352 deviation for trait  $i$  and  $j$ , respectively. Figure 5 clearly shows how misleading such a calculation can  
 353 be using the parameters (i.e., same economic weights, same variances, same accuracy of selection and  
 354 same covariances) already described for a breeding goal with up to 20 traits. The relative emphasis for  
 355 individual traits in a breeding goal should be expressed based on expected response to selection which  
 356 can be derived using selection index theory. Another example can be used to emphasise the point.  
 357 Assume a two-trait breeding goal that includes protein yield and reproductive performance with a  
 358 genetic correlation of -0.50 (Berry et al., 2014b) between them and each with an accuracy of selection  
 359 of 0.99. The same genetic variance is assumed to exist for both traits but the economic weight on  
 360 protein yield is twice that for reproductive performance. No genetic gain in reproductive performance  
 361 is expected with such a breeding goal but the relative emphasis on reproductive performance  
 362 calculated using the approach just described is 33%.

363 It should also be recognised that because of the linearity of breeding goals, there is a plane  
 364 along with the expected response to selection in profit is equivalent, yet the relative weighting (and  
 365 thus expected responses to selection) on the different components of the breeding goal may differ  
 366 subtly. This is depicted in Figure 6 where the straight line represents an axis of equal expected profit

367 response to selection. Point X and Y therefore should be equally profitable yet the expected response  
368 to selection on the input traits at point Y is almost double that of the breeding goal represented at  
369 point X while the expected responses to selection for the output trait is only approximately 20% less.  
370 Such changes may be the difference between a breeding goal being accepted by industry or not.

371 A final consideration in the development of breeding goals is the definition of the trait used in  
372 the breeding goal. There is an on-going debate on whether RFI or feed intake should be included in  
373 the breeding goal for dairy and beef cattle. If appropriately undertaken, and the performance traits  
374 included in the regression for the generation of RFI are also included in the breeding goal, then both  
375 approaches are equivalent (Kennedy et al., 1993). Table 1 describes some of the advantages and  
376 disadvantages of including either feed intake or RFI in a breeding goal. The decision on which  
377 strategy to adopt may vary depending on how it will be eventually used and breeders' understanding  
378 of the different concepts (Wulfhorst et al., 2010). More importantly however is that the policy of  
379 selection for lower feed intake (or RFI) must be undertaken within the context of a holistic breeding  
380 objective. Energy balance and RFI, for example, are strongly positively correlated (McParland et al.,  
381 2014) and therefore selection for reduced RFI (or DMI while also selecting for increased production)  
382 will thrust the cow into more severe negative energy balance which will have disastrous repercussions  
383 for animal well-being and reproductive performance (Beam and Butler, 1999; Collard et al., 2000),  
384 and thus profit.

385

### 386 **Strategies to achieve genetic gain – what do we need?**

387 Dairy cow breeding programs are currently undergoing a paradigm shift with the widespread  
388 incorporation of low-cost genomic information into national genetic evaluations (Hayes et al., 2009;  
389 Spelman et al., 2013). The exploitation of this genomic information is resulting in more rapid genetic  
390 gain but also offers exciting new opportunities to increase performance further for a wider range of  
391 traits, especially if undertaken in conjunction with other (developing) technologies. All national dairy  
392 cow breeding goals in Holsteins constituted solely of milk production traits prior to the mid 1990's.  
393 Almost all dairy cow breeding goals now include other functional traits, in particular reproductive  
394 performance and animal health (Miglior et al., 2005). The relative emphasis on these traits differ by  
395 production system. Missing suites of traits from most, if not all, breeding goals include product  
396 quality, feed intake, and environmental footprint. Animal health is also poorly represented in most  
397 dairy cow breeding goals. The earlier discussions on the ideal cow for the future suggest that national  
398 cow breeding objectives are sub-optimal. Strategies exist, however, to rectify this. This section will  
399 particularly focus on strategies to achieve gains in these suites of traits.

400

401 *Phenotyping strategies*

402 Producers will only record or pay for a phenotype if 1) it helps them improve herd  
403 profitability through the exploitation of greater knowledge, 2) they are financially incentivised to do  
404 so, 3) they are legally required to do so or participation in a scheme (e.g., quality assurance scheme)  
405 requires them to do so, or 4) if they are simply curious or have a desire to help achieve national  
406 objectives.

407 Access to a biological sample (i.e., milk) approximately twice daily provides huge potential  
408 opportunities for routine phenotyping of dairy cows. Developments and mining of transcriptomic,  
409 metabolomic and proteomic information can be used to identify indicators of the biological state of  
410 the cow which can subsequently be incorporated into targeted phenotyping tools. Heritable genetic  
411 variation is known to exist for the milk metabolome (Wittenburg et al., 2013) and proteome (Schopen  
412 et al., 2009). Milk mid-infrared (MIR) spectroscopy has recently been advocated as a useful tool to  
413 predict milk quality attributes (Soyeurt et al., 2011, 2012), cow energy balance (McParland et al.,  
414 2011), feed intake (McParland et al., 2011), feed efficiency (McParland et al., 2014), methane  
415 emissions (Dehareng et al., 2012) and milk urea nitrogen (Godden et al., 2000). Because MIR is  
416 routinely used to quantify milk fat, protein and lactose concentration on all milk recorded cows, the  
417 marginal cost of implementing prediction equations for other milk and animal characteristics is  
418 negligible once accurate prediction equations have been developed. Milk MIR therefore could be a  
419 very useful tool supporting the inclusion of novel traits reflecting milk quality, feed intake and  
420 efficiency, and environmental footprint in futuristic breeding goals. Absorption of light in the MIR  
421 regions corresponds to fundamental bands of molecular vibrations, whereas absorptions in near infra-  
422 red (NIR) region correspond to overtones and combinations of these fundamental bands (Williams  
423 and Norris, 1987). Near-infrared spectroscopy however is more amenable to in-line measurement and  
424 thus could possibly also be useful in the low-cost, rapid and routine measurement of these quality and  
425 animal characteristics at each milking for each animal.

426 The future may require producers to be (financially) incentivised to record novel traits (e.g.,  
427 feed intake) as the benefits of the information to the producer may not be immediately recognised.  
428 The cost-benefit of embarking on such a phenotyping strategy must however be appropriately  
429 quantified taking cognisance of alternative, lower-cost predictors including the example of milk MIR  
430 already discussed. The prediction accuracy for the goal trait does not need to be near unity. The  
431 genetic correlation between milk protein yield and calving interval (i.e., reproductive performance) in  
432 dairy cattle was calculated by Berry et al. (2014b) in a meta-analysis of eight studies to be 0.50.  
433 Despite this, considerable (unintentional) dis-improvement in reproductive performance was achieved  
434 as an artefact of breeding strategies for increased production. Therefore, predictor traits correlated  
435 with the goal trait are useful in breeding goals; the reliability of the genetic evaluations of the goal

436 trait however will never be greater than the square of the correlation with the predictor trait unless  
437 (phenotypic or genomic) information on the goal trait also exists. As previously discussed, inclusion  
438 of a (predicted) goal trait with low reliability will not impact greatly on the genetic gain in the other  
439 traits. Using feed intake in growing heifers as a predictor of feed intake of cows (Macdonald et al.,  
440 2014) could be a useful strategy for including feed intake in lactating cows in the breeding goal since  
441 disruption to normal routine for the measurement of feed intake is likely to have less impact in  
442 growing heifers than lactating cows.

443 Selection index theory can be used to combine several predictor traits in a multiple regression  
444 approach to predict the goal trait. Berry and Crowley (2013) using information on four commonly  
445 recorded performance traits within a selection index framework, reported that 89% of the genetic  
446 variation in feed intake in lactating dairy cows could be explained. Berry and Crowley (2013)  
447 proceeded to suggest that relatively simply implementable technologies like sensors at the feed bunk  
448 to measure feeding activity, or measurement of heat loss, could aid in predicting some of the  
449 remaining unexplained variation. The marginal benefit in accuracy of selection from measurement of  
450 the gold standard feed intake phenotype may actually be low relative to the cost; this needs to be  
451 quantified.

452 Considerable research is also underway on more refined measures of reproductive  
453 performance (Carthy et al., 2013; Walsh et al., 2014) as a means of increasing the heritability of  
454 reproductive performance. As previously alluded to however, it is not heritability *per se* which is  
455 important, it is genetic gain. Therefore if the more heritable reproductive traits are not easily amenable  
456 to large scale phenotyping, or incur a cost of phenotyping, then a benefit to such endeavours may not  
457 exist. The exception is if the heritability of the novel reproductive phenotypes is considerably larger,  
458 eliminating the necessity for phenotyping on a large population of animals. Furthermore, a more  
459 heritable phenotype may be advantageous in the selection of heifers for retention in a herd since the  
460 heritability is a reflection of how closely the genotype reflects the phenotype of an animal; the  
461 correlation between the observed phenotype and unobserved breeding value of an animal is the square  
462 root of the heritability.

463

#### 464 *Genomics*

465 Genetic evaluations and genomic evaluations to date have unashamedly exploited a “black  
466 box” approach (Hill, 2010) where knowledge of the underlying genomic architecture governing  
467 phenotypic differences among animals was unknown. The progress however in all species has been  
468 immense (e.g., <https://www.cdcb.us/eval/summary/trend.cfm>). Weaknesses of quantitative genetics  
469 approaches based on exploiting knowledge on the expected relationships among animals include

470 (Berry et al., 2011b): 1) the phenotype measured contains error (i.e., low heritability trait), 2) the  
471 phenotype may not be measurable in both genders (e.g., milk yield in dairy cattle), 3) adult  
472 performance cannot be measured in juveniles although it can be predicted and some traits like  
473 longevity require a long time horizon to measure, 4) the animal may need to be sacrificed to obtain the  
474 phenotype, 5) antagonistic genetic correlations between traits of interest cannot be easily resolved,  
475 especially in young animals, and 6) genotype by environment interactions may exist, which may  
476 complicate the statistical analysis. Furthermore, the estimation of accurate breeding values requires  
477 the use of large and expensive breeding schemes such as progeny testing. Exploitation of genomic  
478 information in breeding strategies can aid in overcoming some of these shortcomings thus achieving  
479 the cow of the future more rapidly. Because genomic information is available from birth, there is no  
480 longer the requirement to wait several years until the female dairy animal start lactating, a further  
481 several years to obtain a phenotype for longevity, and also several years for the beef merit of the cow  
482 herself or her descendants to be observed. Genomic information is particularly useful in the  
483 generation of estimated breeding values for novel traits such as milk quality, feed intake,  
484 environmental footprint and animal health. Genomic information, however, for the foreseeable future  
485 will not negate the requirement of routine phenotypic information on these traits to achieve high  
486 accuracy of selection.

487         One of the main complications hindering rapid genetic progress in dairy cattle is the genetic  
488 antagonisms (Berry et al., 2011a; Berry and Crowley, 2013; Berry et al., 2014b) between output traits  
489 (i.e., milk production) and cost of production traits (i.e., health and fertility). Genetic correlations are  
490 a manifestation of either the same genomic mutation affecting both traits (termed pleiotropic effect) or  
491 different genomic mutations affecting both traits but tending to, on average, be inherited together (i.e.,  
492 linkage). Selection affects genetic correlations, and if selection has been for improvements in both  
493 traits (e.g., milk production to feed new born and reproduction success to generate the next  
494 generation) the correlation is expected to become unfavourable (Falconer and Mackay, 1996), as  
495 currently observed in dairy cattle (Berry et al., 2014b). This is because the pleiotropic alleles acting  
496 favourably on both characteristics will become quickly fixed under selection; these alleles will thus  
497 contribute little to the variation or the covariance between the two characters. Alleles that affect both  
498 animal characteristics in opposing direction will remain in intermediate frequencies and therefore  
499 contribute more to the covariance between the traits; this also however implies little response to  
500 selection (Falconer and Mackay, 1996). Because rapid selection for increased milk production and  
501 reproductive performance is successful (Berry et al., 2014b), this suggests that considerable  
502 exploitable covariance still exists which could be due to pleiotropy or linkage. Exploitation of  
503 genomic information can aid in elucidating the genomic architecture underlying estimated genetic  
504 correlations; the component of the antagonistic correlation attributable to linkage may be resolved  
505 using the appropriate genomic information. This may result in a weakening of the genetic correlation

506 between favourable performance characteristics and unfavourable reproductive performance. Such an  
507 approach is particularly important for example for traits like feed intake and milk production where  
508 the goal is to change the positively correlated traits (Berry and Crowley, 2013) in opposite directions.

509 Genomic information is currently included in national dairy cow genetic evaluations using, in  
510 most cases, an unsupervised statistical approach; this approach is commonly termed genomic  
511 selection (Meuwissen et al., 2001) and the practicalities of implementing genomic selection for cattle  
512 has been discussed in detail elsewhere (VanRaden, 2008; Hayes et al., 2009; Calus, 2010). Many  
513 studies are on-going in search of the underlying causal mutations affecting phenotypic performance.  
514 The justification for such endeavours are usually to breed better animals through more informed (i.e.,  
515 supervised) breeding schemes or “genotype building” (Dekkers and Hospital, 2002). Access to large  
516 databases of sequence data, once accompanied by large quantities of associated accurate phenotypes,  
517 will expedite the process. Studies have nonetheless been successful in detecting genomic regions  
518 harbouring unfavourable (e.g., lethal) mutations using just genomic information without necessarily  
519 associated phenotypic information (VanRaden et al., 2011). Detection of genomic variants that affect  
520 a large proportion of the genetic variation will remain a considerable and expensive endeavour.  
521 Moreover, even if allelic variation underlying a large proportion of the genetic variation is detected,  
522 this still represents just a small proportion of the phenotypic variation for low heritability traits. Many  
523 other potential outlays for knowledge of the underlying causal mutations and associated genes or gene  
524 networks therefore must be considered (Figure 7) which can be used to generate and manage the cow  
525 of the future.

526

### 527 *Genomics and precision mating*

528 Dairy cattle breeders have traditionally concerned themselves with the exploitation of additive  
529 genetic merit of individuals, because it is the additive allelic effects which are transmitted directly  
530 across generations. Non-additive genetic variation (i.e., inter- and intra-locus interactions) also  
531 contribute to the phenotypic variance (Wall et al., 2005; Sun et al., 2013) and has been successfully  
532 exploited through crossbreeding by, in particular, the New Zealand dairy industry (Lopez-Villalobos  
533 et al., 2000). Heterosis from the mating of two individuals is due to intra-locus effects (i.e.,  
534 dominance) and inter-locus effects (i.e., epistasis). Therefore, the total genetic merit of an animal is a  
535 function of its additive genetic merit (i.e., estimated breeding value), dominance merit, and epistasis  
536 merit. The number of possible epistatic interactions in the genome is unwieldy but can be partly  
537 resolved as more causative mutations are detected. Locus-specific dominance effects can however be  
538 estimated simultaneously with allelic additive genetic effects (Su et al., 2014). The predicted  
539 probability of the genotype of the progeny from a mating can be determined from the respective  
540 genotypes of the parents; for example, the predicted probability of a homozygous, heterozygous, and



541 opposing homozygous genotype in the progeny of heterozygous parents is 0.25, 0.50 and 0.25,  
 542 respectively. The merit of each locus genotype (i.e., additive genetic effect plus dominance effect for  
 543 heterozygous state) can then be summed across the predicted probability of each genotype to generate  
 544 a total genetic merit of an individual. Summed across all traits in the breeding goal, such information  
 545 can be used to identify the specific combining ability for an individual mating or the general  
 546 combining ability of a particular animal (e.g., bull) when mated to another group of animals (e.g., cow  
 547 herd). Such calculations encapsulate both mate complementarity and heterosis effects.

548 Inbreeding occurs when related animals are mated and the resulting inbreeding depression is  
 549 known to impact animal performance (Smith et al., 1998; McParland et al., 2007). The inbreeding  
 550 level of an animal, or coancestry between a pair of individuals, has heretofore been calculated from  
 551 pedigree where it is assumed that full-sibs for example, share, on average, half their genome identical  
 552 by descent (assuming the parents are not inbred). The actual proportion of the genome shared by full-  
 553 sibs (same principle for other relatives) can differ; the standard deviation around this expectation is  
 554 four percentage units in humans (Visscher et al., 2006). Genomic information can therefore be used to  
 555 more accurately quantify the genomic relationships among animals (Pryce et al., 2012). For example  
 556 it is theoretically possible (but extremely unlikely) that two full sibs from non-inbred parents can be  
 557 completely unrelated; similarly an individual can be completely unrelated to one of its grandparents.  
 558 Although the examples given are extreme examples and highly unlikely, it does emphasise that  
 559 mating of traditionally thought of “highly related” animals may not result in high levels of inbreeding.  
 560 This is particularly true at the individual locus level where the presence of lethal or unfavourable  
 561 mutations (VanRaden et al., 2011) within a family can be controlled through designed matings  
 562 without the necessity for blanket culling of carrier animals.

563

564 *Combined genomics and reproductive technologies strategies*

565 Reproductive technologies have a huge potential role in increasing the annual rate of genetic  
 566 gain in dairy cattle mainly through increased intensity of selection (i.e., numerator) and reducing the  
 567 generation interval (i.e., denominator). In reality there are four selection pathways influencing  
 568 population genetic gain:

$$\Delta G_{YR} = \frac{(i_{SS} \cdot r_{SS} + i_{SD} \cdot r_{SD} + i_{DS} \cdot r_{DS} + i_{DD} \cdot r_{DD}) \cdot \sigma_G}{L_{SS} + L_{SD} + L_{DS} + L_{DD}}$$

569 Where  $\Delta G_{YR}$  is annual genetic gain,  $i_{**}$  is the standardised selection intensity for the \*\*  
 570 pathway,  $r_{**}$  is the accuracy of selection for the \*\* pathway,  $\sigma_G$  is the genetic standard deviation  $L_{**}$  is  
 571 the generation interval for the \*\* pathway; the pathways SS, SD, DS and DD represent sire-to-sire,  
 572 sire-to-dam, dam-to-sire and dam-to-dam, respectively. Because genomic information can be used to

573 generate an accurate prediction of the genetic merit of an animal at birth, one of the current limiting  
574 factors in the sire to produce progeny pathway is the age at which sufficient high quality semen can be  
575 obtained from young bulls and used in the population without compromising reproductive  
576 performance. This requires research on optimal pre- and post-pubertal management strategies of bulls  
577 as well as optimum cryopreservation and management strategies of the semen.

578 Cow natural reproductive rate limits the annual number of progeny per cow. Advances in  
579 ovum pick up and in vitro fertilisation techniques circumvent the necessity to wait for sexual maturity  
580 of potential dams thereby reducing the dam to produce progeny generation interval and increasing  
581 overall annual genetic gain. These approaches, coupled with multiple ovulation embryo transfer and  
582 embryo genotyping (Humboldt et al., 2010), can also be used to reduce further the generation interval  
583 of the dam to progeny pathway while also increasing the respective selection intensity; such processes  
584 can also increase the selection intensity of the sire to progeny pathways.

585 To accelerate genetic gain, low cost semen sexing or gender-biasing technologies producing  
586 normal conception rate are required. Not alone will access to sexed semen improve genetic progress,  
587 but it can also improve animal welfare by reducing the incidence of dystocia in dairy cattle where  
588 (lighter) females are generally sought after. In addition, productivity could be increased, and the  
589 environmental impact reduced by having less productive or unwanted male animals.

590

#### 591 *Combined genomics and management strategies*

592 Pharmacogenomics is the study of how the response to medicinal intervention is affected by  
593 the genome of the individual; the outcomes from this discipline facilitate the development of tailor-  
594 made health programs for individuals differing in their underlying genome. For example, it may be  
595 decided to use dry cow therapy only on cows with a greater genomic risk of succumbing to udder  
596 infection in the following lactation. Nutrigenomics is the study of the effect of nutrition on gene  
597 expression, or in other words, the effect of the genome of the animal on response to alternative  
598 nutritional supplements. On-going dairy cow breeding programs have, and continue to take advantage  
599 of nutrigenomics at the macro level by selecting, for example, animals in confinement production  
600 systems that respond more to concentrate input. Controlled experiments have clearly showed than  
601 animals of superior genetic merit for milk production (generally of North American ancestry) yield a  
602 greater milk production response to concentrate input compared to animals of lower genetic merit for  
603 milk production (Dillon et al., 2006). Genomics will facilitate more accurate identification of suitable  
604 animals for different production systems. I define reproductomics here as the study of how the genome  
605 of the animal affects its response to alternative reproductive treatments (e.g., oestrus synchronisation  
606 treatments) or in other words the tailoring of reproductive treatments (if required) to the genome of

607 the individual cow. Also included in this could be the receptiveness of individual cows to sexed  
608 semen; no information exists on whether genetic predisposition of individual cows to  
609 conception/pregnancy with sexed semen versus conventional semen exists although heritable genetic  
610 variation in sex ratio is known to exist (Berry et al. 2011b). It is unlikely, however, that any single  
611 mutation or small number of mutations will control a large proportion of the genetic variation in  
612 response to medicinal, nutritional or reproductive intervention in cattle and thus such strategies 1) will  
613 firstly require a huge amount of data to quantify the genetic by environmental effects, 2) segregation  
614 of animals for different management protocols will still have to be taken at the macro (i.e., estimated  
615 genetic value) level, albeit with greater accuracy to achievable heretofore.

616

### 617 *Sentinel herds*

618 Lessons from the past dictate that performance of genetically elite animals for a breeding goal  
619 should be continuously monitored and compared to lower genetic merit animals. Elucidation of any  
620 deleterious impacts of selection is arguably best achieved under controlled environments in a limited  
621 population where more detailed, or more expensive measurements, can be routinely undertaken.  
622 Moreover, health events are usually measured once the animal is in a clinical state but observations at  
623 the sub-clinical level can be used as an early alert of the long-term consequences of selection.  
624 Detailed -omic technologies (e.g., transcriptomics, metabolomics, proteomics) undertaken on different  
625 biological samples from a limited number of animals can be extremely beneficial to predict what the  
626 likely consequences of selection are several generations hence. These sentinel herds are different to  
627 nucleus herds since they must also consist of a control group for comparative purposes but also some  
628 of the interventions required to decipher the impacts of selection (e.g., biopsies, infection with  
629 pathogens) may impact animal performance which will subsequently impact the estimated genetic  
630 merit of the animal. Although including contemporary group in the genetic evaluation model may aid  
631 in eliminating these effects, the possible carryover of effects and interactions between effects may  
632 bias the genetic evaluations. While sentinel herds are expensive to operate, they should be viewed as  
633 an important insurance policy for breeding programs.

634

### 635 **Breeding landscape of the future?**

636 The rapid advancements in ‘-omic’ technologies and reproductive technologies necessitates a  
637 reassessment of modern-day breeding programs. Individual breeders in some countries can now  
638 receive genomic evaluations for their individual bulls, and therefore can obtain accurate estimates of  
639 genetic merit for routinely measured traits for tens of dollars compared to several thousands of dollars

640 prior to the implementation of genomic selection. AI breeding companies must therefore identify  
641 additional added value for their bulls over and above the obvious like selling quality assured semen as  
642 well as access to sexed semen. Another value added resource may be accurate genetic/genomic  
643 evaluations for difficult to measure traits not already included in the national breeding objectives and  
644 thus not available to competing AI companies and breeders.

645         Although international sharing of phenotypic (Berry et al., 2014a) and genomic (Pryce et al.,  
646 2014) information for the derivation of international genomic evaluations of expensive to measure  
647 traits like feed intake is a plausible strategy, high accuracy of selection for the component of feed  
648 intake net of predictor traits is unlikely to be achievable. Furthermore, large scale phenotyping for  
649 gold standard feed intake measures in commercial herds is unlikely. Therefore, it is likely that the  
650 number of performance (or progeny) test centers may increase. Because the heritability of feed intake  
651 in lactating dairy cow is relatively high (0.10 to 0.54; Berry et al., 2007; Berry et al., 2014a;  
652 Veerkamp and Thompson, 1999), not many records are required to achieve high accuracy of selection.  
653 The reliability of a univariate genetic evaluation for feed intake where the animal itself has a feed  
654 intake observation (ignoring parental contribution) is the heritability; this is likely to be greater with  
655 the incorporation of genomic information once the reference population to estimate the allele effects  
656 is large and related to the candidate population (Habier et al., 2007; Pszczola et al., 2012). Only two  
657 studies have attempted to estimate the genetic correlation between feed intake in growing females and  
658 lactating dairy cows (Nieuwhof et al., 1992; Berry et al., 2014a); the genetic correlation is 0.67 to  
659 0.74. Within a nucleus herd environment it may therefore be possible to phenotype the cow for feed  
660 intake during lactation. These data could be used to generate genomic evaluations for feed intake on  
661 candidate bulls which could be supplemented with actual feed intake records on the candidate bull  
662 itself during pre-pubertal growth; the feeding regime imposed should not affect subsequent semen  
663 production or quality. Moreover, consideration should be taken on the timing of the performance test  
664 relative to puberty, as bulls that reach puberty during the test may be expected to eat more and may  
665 subsequently be viewed as being poorly efficient. Methane emissions could also be simultaneously  
666 measured on all animals.

667         Consideration could also be given to measurement of novel traits on siblings; depending on  
668 the phenotype, it may be possible to measure performance of the entire group rather than individually  
669 thereby saving resources. Full or half-sib groups can be generated using MOET and some of the  
670 siblings sacrificed for phenotyping. An example of such an approach may be the inoculation of full-  
671 sib or half-sib males with pathogens and the animal response(s) measured; such approaches are  
672 successfully implemented in genetic evaluations of disease resistance in aquaculture (Ødegård et al.,  
673 2011). Although the maximum reliability achievable using traditional quantitative genetics from  
674 measurement on full-sibs (half-sibs) is 0.50 (0.25), genomic predictions derived from the phenotyped  
675 siblings could aid in achieving considerably higher accuracy of selection. This design is particularly

676 useful as the reference population would be clearly related to the candidate population thereby  
677 achieving a high accuracy of genomic prediction (Habier et al., 2007; Pszczola et al., 2012).

678 Intellectual property leakage is of increasing concern among breeding companies who invest  
679 considerable resources in the development of a genetically elite product (e.g., breeding values for  
680 novel traits). Semen from these genetically elite bulls, however, may be used by competitors to  
681 generate bull descendants with the elite characteristics. Figure 8 shows how a base population can be  
682 rapidly upgraded to another (elite) population; within 3 generations the upgraded population contains,  
683 on average, 87.5% of the elite population which increases to 93.75% in generation 4. This process can  
684 be intensified through the exploitation of reproductive technologies (i.e., ovum pickup plus in vitro  
685 fertilisation) and the rate of upgrading can also be increased through exploitation of genomic  
686 information to retain animals with a greater proportion of the elite genetic line. Other than the  
687 necessity of invoking legislation to prevent such efforts, the marketing of female-only sexed semen  
688 will retain ownership of the proprietary lines, ensuring the necessary return on investment (at least in  
689 the short to medium term). Even if a male calve results, it possess only half the genome of the elite  
690 line and its progeny only, on average, a quarter of the genome.

691 Artificial insemination has revolutionised dairy cattle breeding since its wide-spread adoption.  
692 AI, however, has only resulted in increased selection intensity in the sire to progeny selection  
693 pathway. Considerable gains in selection intensity, and thus genetic gain, could be achieved by  
694 applying similar principles to the dam to progeny selection pathways. This would involve a large  
695 scale generation of embryos or female progeny for sale to elite breeders which in turn could act as  
696 multiplier herds for commercial producers. Parents or siblings of the embryos could be phenotyped  
697 for novel traits and genomic predictions derived; the embryos could be genomically screened and  
698 sexed and the price requested tiered based on genetic merit. Moreover, favourable epigenetic effects  
699 could be sought by implanting the embryos into unstressed surrogate dams.

700

## 701 **Conclusions**

702 The first step in breeding for the cow of the future is to agree on the characteristics that  
703 describe that ideal cow and the relative importance of each of those characteristics. Because of genetic  
704 antagonisms, it may not be possible to achieve ideal performance for each characteristic. Acquisition  
705 of phenotypic data remains one of the key components for achieving high accuracy of selection and  
706 thus genetic gain, even in the genomics era. Key suites of traits warranting immediate inclusion in  
707 dairy cow breeding goals include product quality, feed intake and efficiency, environmental footprint  
708 and animal health.

709

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967 Table 1. Reasons in favor and against including dry matter intake (DMI) or residual feed intake (RFI) in a  
 968 breeding goal

DMI in the breeding goal	
For	Against
Easy to explain and understand	Cannot easily identify efficient animals
Economic value is relatively easy to calculate	May be mis-understood (positive EBV may be efficient)
Amenable to customised indexes	Correlated with performance
Economic value on other components reflect reality in the market place (e.g., fat:protein price ratio)	Independent culling levels may be harmful to overall gain Misinterpreted that negative EBV might imply poorer performing animals
Good predictors available	
Higher "reliability" through selection index theory	
May be less susceptible to genotype by environment interactions (GxE)	
RFI in the breeding goal	
For	Against
Economic value is relatively easy to calculate	Difficult to explain technically
Can "easily" slot in to current breeding goals	Low reliability (currently)
(Theoretically) uncorrelated with performance	Possibly more susceptible to GxE
Relatively simple message (if not caught up in details)	Selection index within a selection index Sensible to select on something we do not understand? (Never stopped us before!)
Could materialize in faster genetic gain for efficiency	Mixed messages from "pro" and "against" camps RFI in lactating animals (as currently defined) is not ideal EBVs may change as the RFI model changes Possibly correlated with fertility (so is DMI!)

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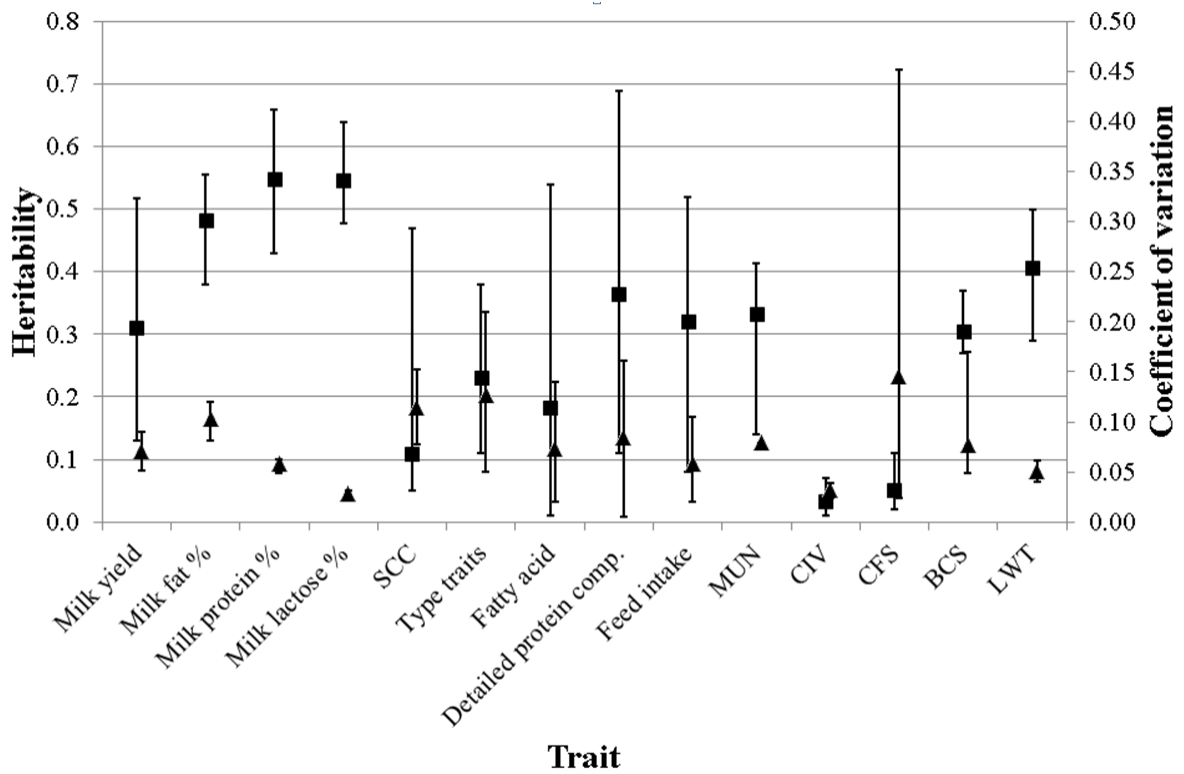
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984 Figure 1. Mean heritability (squares) and coefficient of genetic variation (triangle) and variation  
985 (represented by error bars) for a range of performance traits including somatic cell count (SCC), milk  
986 urea nitrogen (MUN), calving interval (CIV), calving to first service interval (CFS), body conditions  
987 core (BCS) and live-weight (LWT)

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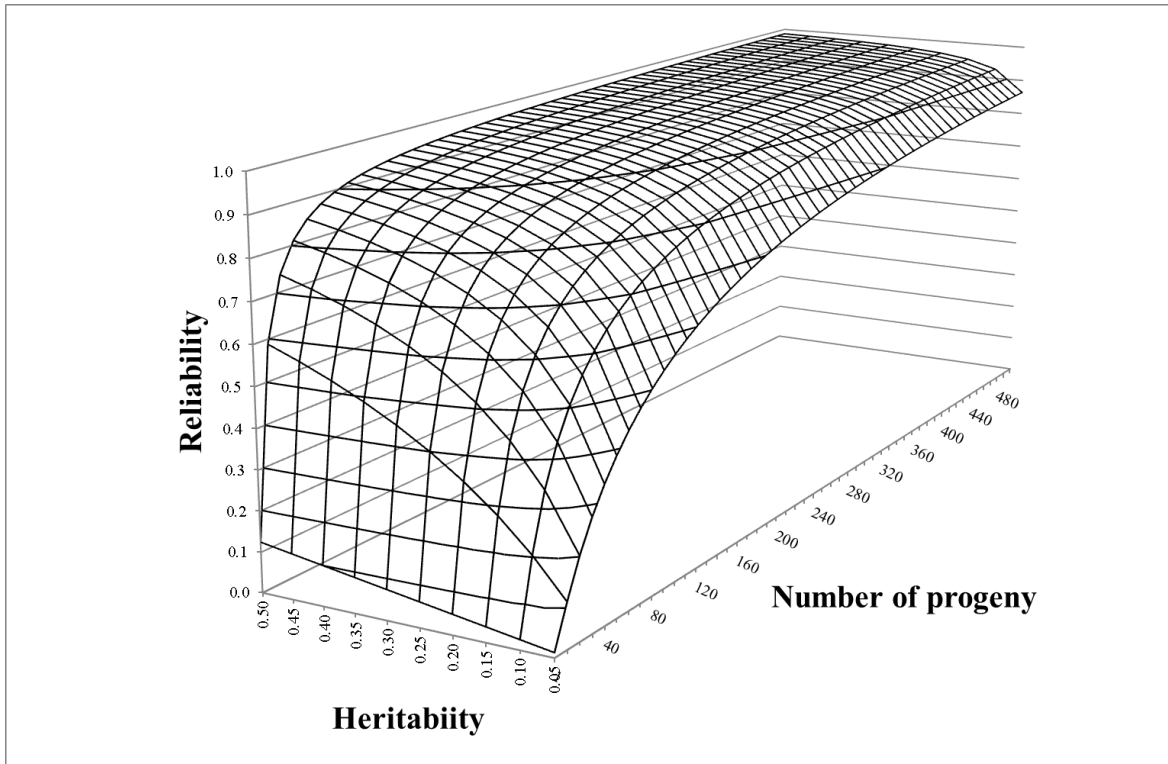
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997 Figure 2. Reliability of univariate genetic evaluations for a single trait of different heritability based  
 998 only performance information for varying numbers of progeny

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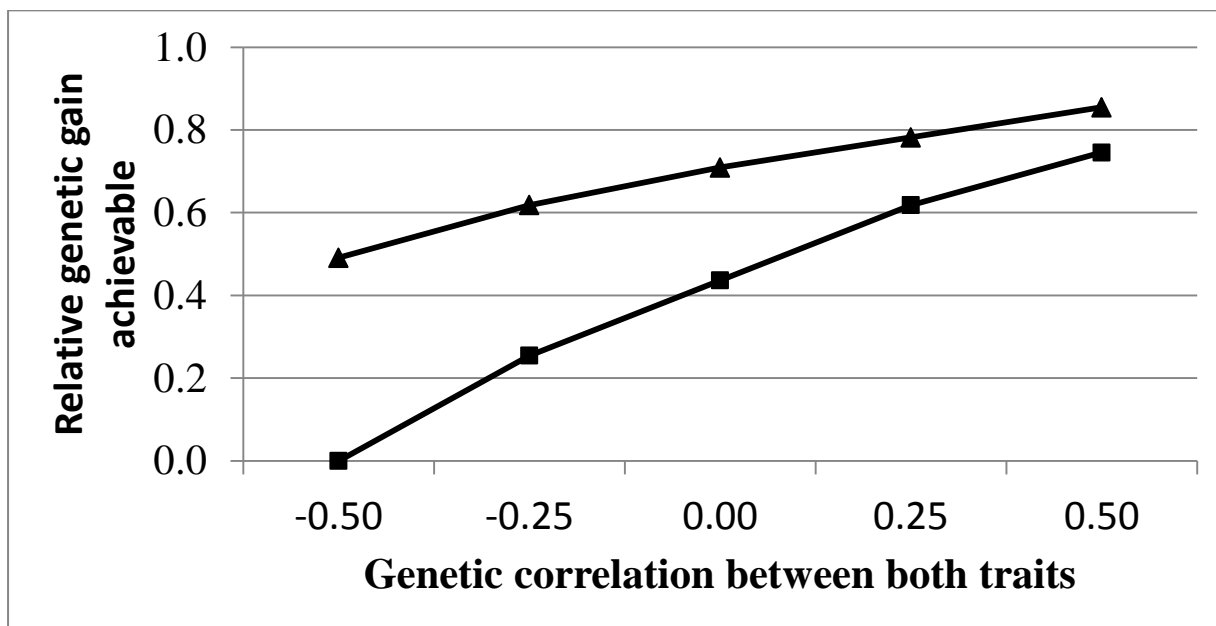
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1013 Figure 3. Expected genetic gain in a given trait in a two trait breeding goal with a second trait with the  
1014 same genetic variance times economic weight as the first trait (triangle) or twice the genetic variance  
1015 times economic weight of the first trait (squares) relative to selection solely on the trait itself;  
1016 accuracy of selection for both traits was assumed to be 0.99.

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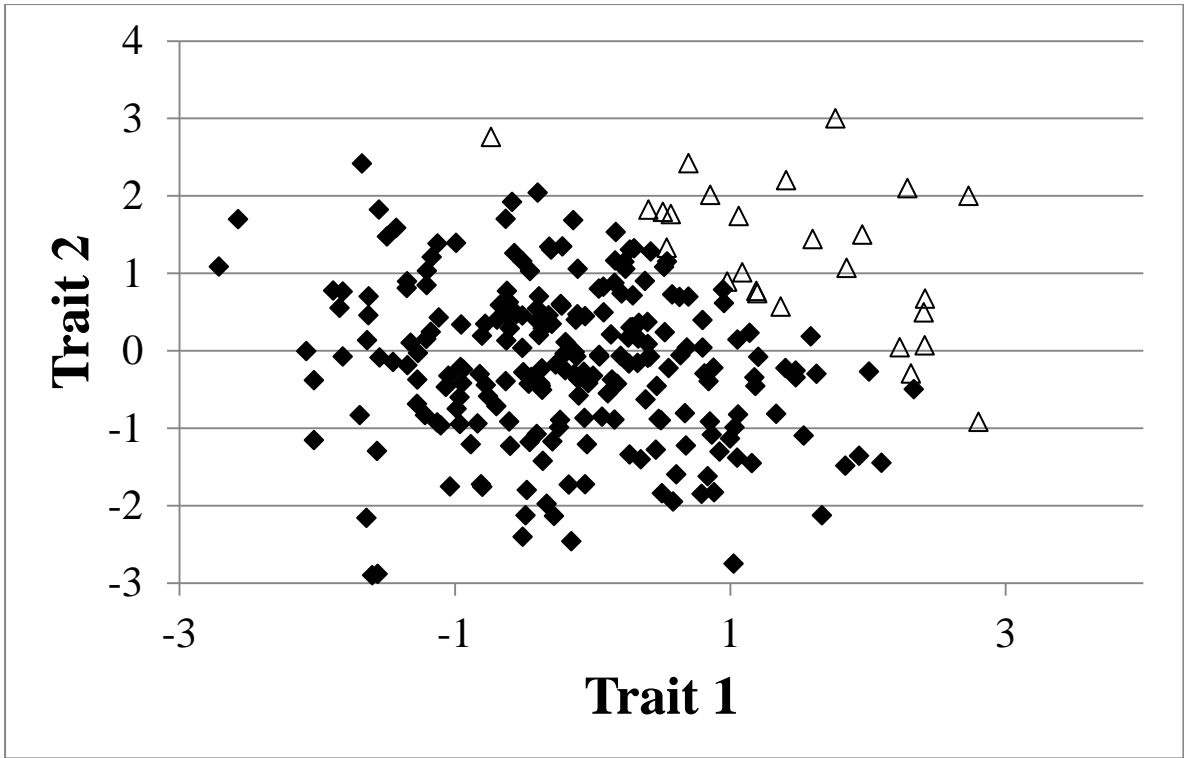
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1030 Figure 4. Scatter plot of two uncorrected traits each standardised to a normal distribution. Triangles  
1031 represent the top 10% of animals ranked on a combination of both traits each with the same  
1032 weighting.

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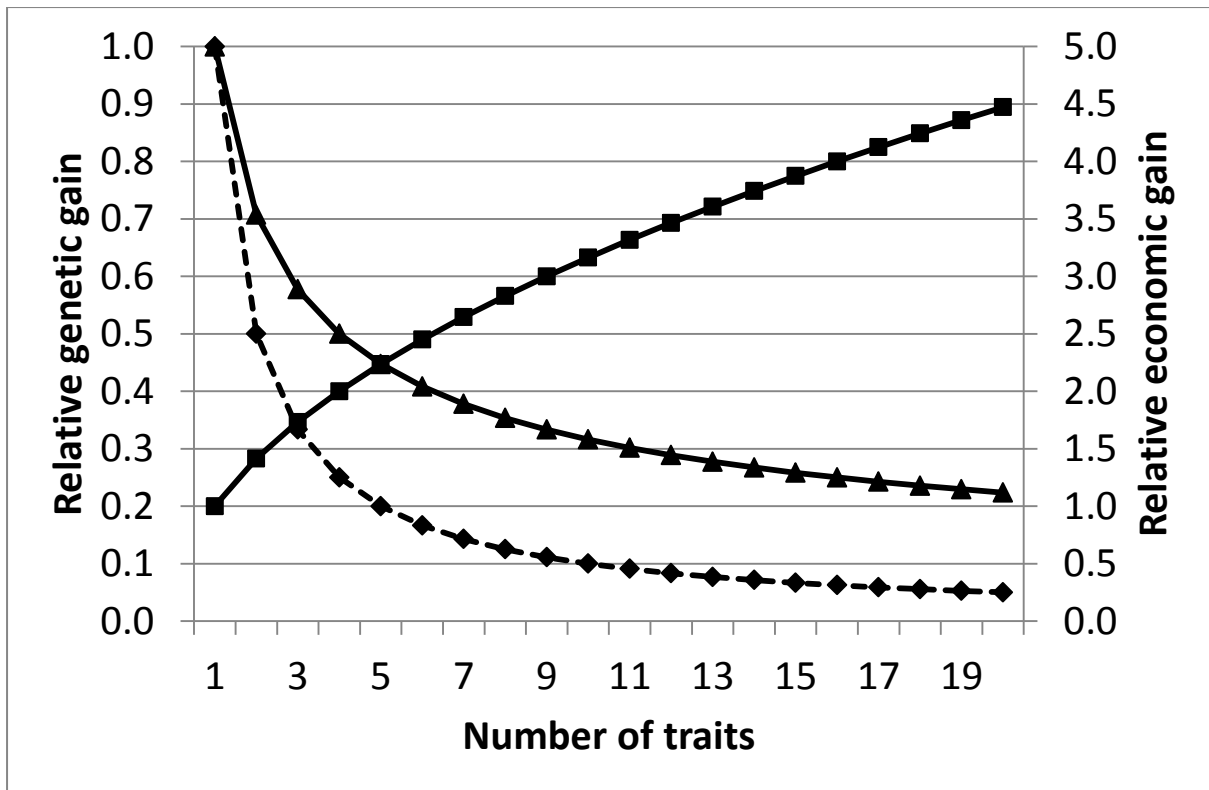
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1044 Figure 5. Expected genetic gain for a given trait as the number of traits included in the breeding goal  
 1045 increases from one to 20 (triangle) assuming equal genetic variance, weighting and accuracy of  
 1046 selection for each trait as well as no covariance between any trait as well as the relative economic gain  
 1047 (squares; per index standard deviation unit) for the entire index assuming an equal economic weight  
 1048 of one on all traits. Also included is the calculated relative emphasis for a trait within the breeding  
 1049 goal differing in number of included traits.

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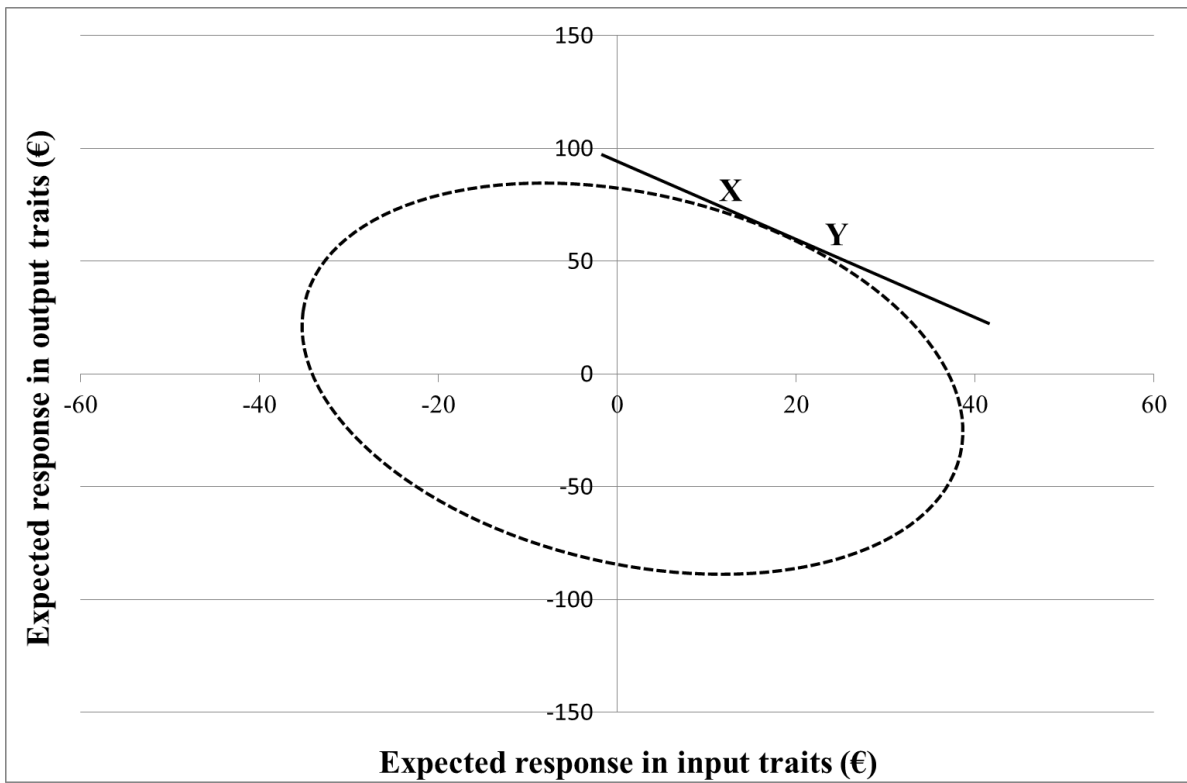
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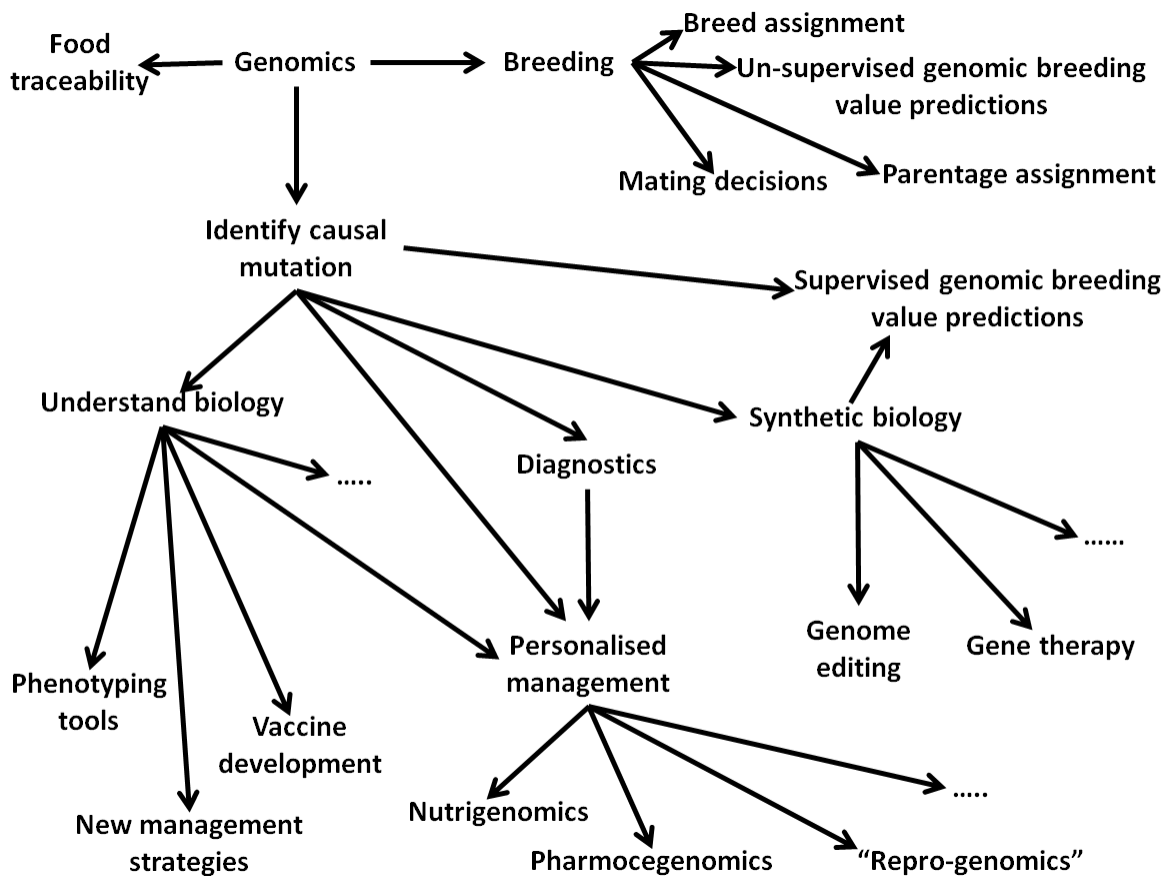
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1059 Figure 6. Comparison of the effect of alternative breeding goals on input and output traits on expected  
 1060 responses in profit. Point X and Y will yield the same expected profit but relative expected responses  
 1061 for the input and output traits differ considerably.



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1065 Figure 7. Potential uses of genomic information in achieving increased animal performance.

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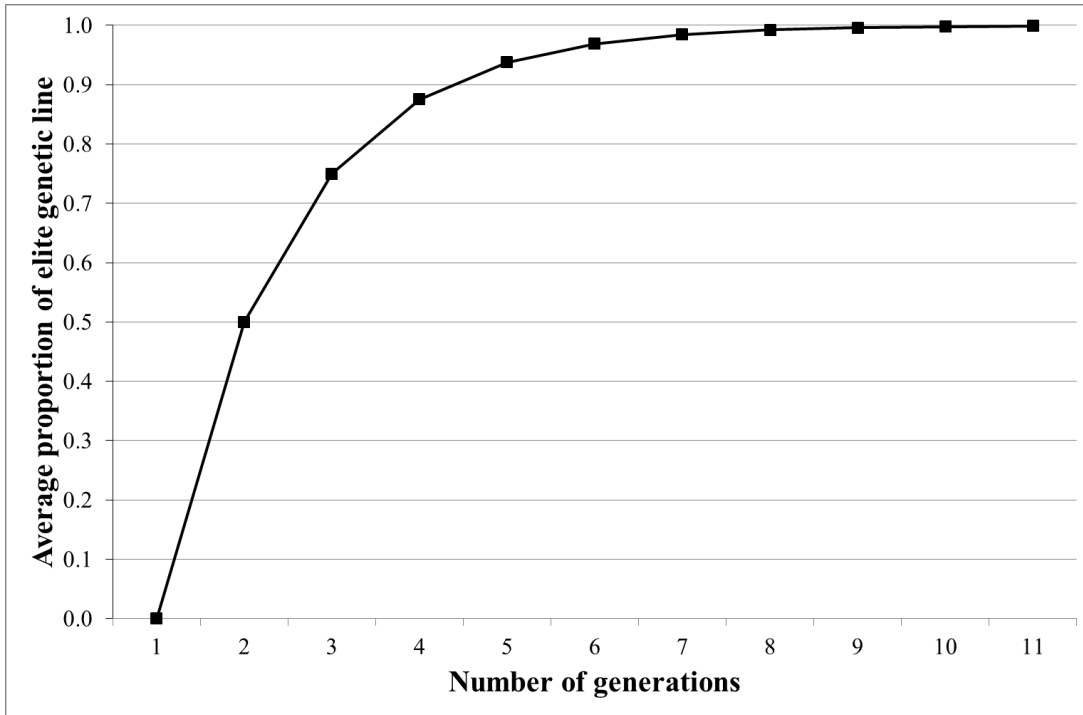
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1076 Figure 8. Average proportion of genetically elite line per generation from upgrading of a population.

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