Breeding schemes for dairy cows under genomic selection – what can we do?

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Introduction

The use of genomic breeding values to make selection decisions when animals are born rather than waiting for phenotypes to become available has substantial implications for the design of dairy cattle breeding programmes (Schaeffer 2006; Goddard, 2009). Modeling suggests annual rates of genetic gain (ΔG) can be increased by 30% to 140% over current ΔG (Schaeffer, 2006; Harris *et al.*, 2008; König *et al.*, 2009).

Genomic selection opens a number of opportunities for new breeding scheme designs. Our aim was to evaluate a broad range of breeding scheme designs incorporating genomic breeding values: including schemes where large numbers of young bull calves are genotyped, nucleus breeding schemes that focus on selection in females and schemes in which candidates are selected across countries on the basis of their GEBV.

Material and methods

The Rendel & Robertson (1950) method of calculating ΔG using four pathways of selection is a convenient way to evaluate the impact of genomic selection (Schaeffer, 2006) The four pathways are sires to breed sires (SS), sires to breed cows (SC), cows to breed sires (CS) and cows to breed cows (CC).

The total response to selection can be calculated using the sum of response to selection over the sum of generation interval in the four pathways of selection:

$$\Delta G = \frac{\sum_{i=1}^{4} SI_i r_i \sigma_{Ai}}{\sum_{i=1}^{4} L_i}$$

Where L_i is the generation interval in the i^{th} selection pathway, SI_i is the selection intensity in the i^{th} pathway of selection, r_i is the accuracy of selection (square root of the reliability) and σ_{Ai} is the genetic standard deviation of selection (assumed to be 1).

Rate of inbreeding The rate of inbreeding per generation (ΔF) was calculated as:

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$$\Delta F = \frac{1}{32\overline{L}}\left[\frac{1}{N_{SS}} + \frac{3}{N_{SC}} + \frac{1}{N_{CS}} + \frac{3}{N_{CC}}\right]$$

Where $\overline{L}$ is $\sum_{i=1}^{4} L_i / 4$ and N_{ss} is the number of new SS per generation etc. Rate of inbreeding per year was calculated as: $\Delta F / yr = \Delta F / \overline{L}$

Design of breeding schemes. The population of breeding cows was assumed to be 140,000, which is representative of the Australian Holstein dairy cow population that is milk-recorded. As a base for comparisons, progeny-testing (PT) was modeled assuming that there were 10 SC and 2 SS selected from a progeny test of 100 sons of 333 cows (Table 1). In PT, the reliability of SS and SC proofs was assumed to be 0.8.

Table 1: Selected individuals versus candidates available for selection, reliability and generation interval (L) for the pathways of selection (SS, SC, CS and CC) for various breeding scheme designs

Scheme	**Assumption**	**Pathway of selection**		
		SS/SC	CS	CC
PT	Selected/Candidates	2/100 SS 10/100 SC	333/140,000	-
	Reliability	0.8	0.32*	-
	L	6.5	3.22	4.94
GS-Y	Selected/Candidates	20/1000	3,333/140,000	-
	Reliability	0.6	0.36*	-
	L	2	3.34	4.94
GS-Y-CC	Selected/Candidates	20/1000	3,333/140,000	65%
	Reliability	0.6	0.36*	0.39*
	L	3	3.36	3.6
GS-WW	Selected/Candidates	20/6000	20,000/840,000	-
	Reliability	0.59*	0.36	-
	L	2	3.34	4.94
GS-CN1	Selected/Candidates	20/300	300/300	300/300
	Reliability	0.6	0.6	0.6
	L	2	1	1
GS-CN2	Selected/Candidates	20/600	300/600	300/600
	Reliability	0.6	0.6	0.6
	L	2	2	2

*Reliability is the weighted mean across age classes

In all schemes under genomic selection we considered 20 males as SS and SC because it was assumed that larger bull-teams would be used in genomic selection to reduce the risk of retrospective poor performance of some sires as reliability increases (through the addition of progeny records). GS-Y is a young bull scheme where there was high selection intensity in male pathways of selection; 1,000 males would be genotyped and these would be the offspring of 3,333 cows (assuming a sex-ratio of 0.5 and a calving rate to AI sires of 0.6). The reliability of genomic selection was assumed to be 0.6. The reliability of females was a weighted average of reliability of selected cows (3,333/140,000) from age classes (1-6) that had 25%, 21%, 18%, 15%, 13% and 8% candidates for selection. Most selected CS were from the youngest age class. GS-Y-CC is the same as GS-Y, except there was selection in the female selection path and heifers were also used to generate replacements. We also explored the impact of sexed semen in this scheme.

In GS-WW it was assumed that genotypes were freely exchanged between six countries (with equal sized populations of dairy cows) increasing the total population available to 840,000 and the number of new genotyped bulls per year was 6,000, this scheme was modelled assuming reliabilities were the same in each country. Finally, a nucleus breeding scheme (GS-CN) was considered where 300 heifers were part of a juvenile in-vitro embryo transfer (JIVET) and multiple ovulation and embryo transfer (MOET) programme. Each heifer would yield either two or four viable offspring per year depending on whether JIVET was performed at one or two years of age (GS-CN1 and GS-CN2 respectively). In closed nuclei selection intensities in the CS and CC pathways are equal.

Results and discussion

For progeny testing (PT), the ΔG achieved was 0.25 σ_A/year (Table 2) and is comparable to published rates of genetic gain for PT (e.g. Schaeffer, 2006), ΔF was 0.18% per year. Rates of genetic gain for schemes that included genomic selection ranged from 1.6× PT to 2.3× PT. This was accompanied by lower ΔF per generation (0.18% to 0.44%) than PT (0.95%) and annually ΔF between 37% and 165% of that of PT. Inbreeding is primarily a function of number selected rather than population size. The reason why the genomic selection schemes (except for nucleus breeding schemes) had lower ΔF than young bull breeding schemes was because of reduced selection intensity in the male pathways, especially in the SS pathway. If the same number of SS and SC are used as PT (10 and 2 respectively), the rate of ΔG achieved in GS-Y would be 0.47 and ΔF/yr would be 0.53%.

Table 2: The annual rate of genetic gain (ΔG) in σ_A units, rate of inbreeding (ΔF) per generation and per year and percent annual rate of inbreeding compared to PT

	ΔG/year in σ_A/year	ΔG/year relative to PT (%)	ΔF/generation	ΔF/year	ΔF/year relative to PT (%)
PT	0.25	100%	0.95%	0.18%	100%
GS-Y	0.40	159%	0.20%	0.066%	37%
GS-Y-CC	0.49	194%	0.18%	0.089%	49%
GS-WW	0.48	190%	0.20%	0.066%	37%
GS-CN1	0.50	199%	0.44%	0.30%	166%
GS-CN2	0.59	231%	0.33%	0.17%	93%

Reducing generation interval had the greatest impact on ΔG (Table 2). GS-Y, where bulls were selected for widespread use at one year of age on the basis of their GEBVs led to a large increase in ΔG (0.40 σA/year). Selection on GS-Y-CC would result in an extra 22% ΔG compared to GS-Y. At present genotyping costs are prohibitive in decisions to genotype entire commercially operated herds, as genotyping costs are likely to far exceed the benefits (Schaeffer, 2006 and König & Swalve, 2009). However, if it was cost-effective, for example using a SNP subset, then selection decisions within herds (i.e. in the CC pathway) using GEBVs will be more attractive. Sexed semen could also be used to improve ΔG, based on a 90% success rate in achieving females, ΔG in GS-Y-CC would increase by 10%.

Compared to the GS-Y scheme, GS-WW would result in an increase in ΔG of around 9% (0.48 σ_A/year). If reliabilities were lower in non-domestic countries, i.e. genotypes were not exchanged and genotype by environment interactions existed resulting in correlations of 0.8 with the domestic country, the response would be 0.41 σ_A/year. GS-WW may be useful where countries have small populations of dairy cows and there are other countries with populations of dairy cattle that are at least as good as the importing country. Or alternatively it may be of interest in countries without a national breeding scheme. It could also be used by minor breeds where selection decisions within country are constrained by population size.

Very high rates of genetic gain can be achieved by reducing generation intervals and applying advanced reproductive technologies in controlled breeding schemes such as GS-CN1 and GS-CN2 (Table 2). However, these schemes can lead to increased rates of inbreeding. Strategies to alleviate inbreeding could include either minimising relationships between individuals or maximising heterozygosity in SNPs not under selection.

Conclusion

Nucleus schemes and "worldwide" schemes where GEBVs were available from foreign countries achieved the greatest ΔG. Even greater responses are achieved if JIVET is used, demonstrating that reducing the generation interval in genomic selection applied to dairy cows is the most effective strategy to maximize ΔG. However, annual rates of inbreeding become prohibitive in very high ΔG nucleus breeding schemes, so tools to control ΔF become more important.

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