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Potential response from selection schemes based on progeny testing and genomic selection for the Chilean dairy cattle under pastoral systems: a deterministic simulation

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Research Article

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Abstract

Recently, a selection index called Valor Económico Lechero (VEL) was developed for Chilean dairy cattle under pasture. However, a specific selection scheme has not yet been implemented. This study aimed to estimate genetic progress from selection on the VEL selection index based on selection schemes using progeny testing (PT) and genomic selection (GS). Under a PT-scheme, estimated genetic progress was 41.50, 3.44, and 2.33 kg/year for milk, fat, and protein yield, respectively. The realised genetic gain takes eight-year after the PT-scheme implementation, which may be a disincentive for implementing a PT-scheme, suggesting that importing frozen semen of proven bulls could be a preferred alternative. In this case, an option may be to conduct the genetic evaluation of those bulls using their progeny in Chile for the traits included in VEL selection index. In the case of implementing a specific selection scheme, compared to PT, a more profitable alternative might be the implementation of a GS-scheme, that would result in a faster genetic gain in the aggregate breeding value or merit for all the traits included in the selection objective (0.323–0.371 *vs.* 0.194 σ_g/year).

Introduction

In Chile, seventy per cent of dairy milk production is produced in the country's southern regions. These regions are Araucania (IX), Los Lagos (X) and Los Rios (XIV). In these three regions, milk production, similar to New Zealand, is mainly based on grazing pastures, where the goal is to obtain high production of milk solids per unit of land rather than milk yield per cow (Uribe *et al.*, 2017).

The selection index as a tool to select animals for breeding replacement has had a major role in breeding programmes for dairy cattle in countries such as New Zealand (Breeding Worth); Ireland (Economic Breeding Index) and the Netherlands (Total Merit Index). In Chile, however, genetic changes in dairy cattle have been achieved mainly by importing frozen semen from proven bulls in other countries to be used in local cows (Verdugo *et al.*, 2004). Technically, this approach corresponds to migration rather than selection (Falconer and Mackay, 1996). This strategy might be advised in the absence of genotype by environmental interaction ($G \times E$) and differences in economic and production circumstances (López-Villalobos *et al.*, 2001) but otherwise could produce sub-optimal genetic progress.

In Chile, a frozen semen importing company recently developed a selection index called Valor Económico Lechero (VEL) (Lama and Vargas, 2020). It will be applied in ranking cows and imported bulls used in dairy cattle breeding in Chile's southern region. The VEL index is calculated by weighing the estimated breeding values (EBVs) for lactation yields of milk (MY), fat (FY) and protein (PY) (production traits), somatic cell score (SCS), age at first calving (AFC), calving interval (CI), and longevity (functional traits), by their respective economic value (Lama and Vargas, 2020).

The selection index (Hazel, 1943) is a method for estimating the total aggregate genetic value of an animal by combining EBVs for traits of economic importance with their corresponding economic values. It is the basis on which the animals are ranked for selection. The optimal selection index maximises the correlation between the selection index (traits recorded as predictor) and the selection objective (traits of interest to improve) (Mrode, 2014). Therefore, selection indices are used as predictors of the selection objective, which is focused on traits that influence the breeding goal. In the VEL index, for example, the traits included in the selection objective are the same as those included in the index. Using the selection index theory, the estimation of genetic changes for the traits in the selection objective can be estimated from selection schemes based on the four pathways of selection (Rendel and

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Robertson, 1950). These pathways are cows to breed cows (CC), cows to breed bulls (CB), bulls to breed cows (BC), and bulls to breed bulls (BB).

Although the VEL index is the first tool developed in Chile to genetically improve the dairy cattle population under pasture, a selection scheme for the Chilean dairy population has not been implemented. Therefore, it is of interest to design a specific selection scheme, because it dictates the potential genetic progress that can be achieved for the traits economically important to improve, and it has considerable influence on the cost-effectiveness of the selection programme (López-Villalobos and Garrick, 2005).

In a dairy selection scheme, the main method of evaluating bulls is progeny testing (PT). However, genomic selection (GS; Meuwissen *et al.*, 2001) makes it possible to modify the conventional PT selection scheme. In this scheme, the rate of genetic gain can be as much as double compared to PT (Schaeffer, 2006). Accordingly, this study aimed to evaluate a selection scheme by estimating genetic progress in the traits included in VEL based on PT or through GS.

Material and methods

Population structure

The dairy cattle population under grazing conditions in Chile (La Araucanía, Los Ríos, and Los Lagos Regions) is around 500 000 cows (ODEPA, 2019). Considering a replacement rate of 30% (Olivares *et al.*, 2012), the theoretical age structure for a typical herd in Southern Chile can be estimated as follows: 30.0% 2-year-olds, 22% 3-year-olds, 16% 4-year-olds, 11% 5-year-olds, 8% 6-year-olds, 6% 7-year-olds, 4% 8-year-olds, 3% 9-year-olds, and 2% 10-year-olds. This results in a 4.0 year-old average age structure.

Derivation of cow and bull paths

Selected cows as bull mothers (CB) correspond to those cows in their second, third and fourth lactations. It was considered that 70% of these cows could be selected. The number of cows required to produce one bull for PT was assumed to be 6.6 times the number of bulls required to be progeny tested (López-Villalobos *et al.*, 2000). The proportion of cows selected (CC) was assumed 99% since generally there are limited opportunities for selection among female replacements. It was assumed that there were two yield records for cows in the CB and CC pathways (Spelman and Garrick, 1997).

The selected proportions in the BB and BC pathways were 10% and 20%, respectively. Each bull was assumed to be evaluated based on the performance of 85 daughters (Spelman and Garrick, 1997). The proportions of selected bulls are greater than those selected in New Zealand (Sneddon *et al.*, 2016), since for small populations (as deemed for the Chilean dairy cattle industry), it would be required to increase the proportion of bulls selected to avoid inbreeding (Lembeye *et al.*, 2021).

Generation intervals calculated for the dairy population were based on the age structure of the population for the CC pathway described above. It was assumed that heifers are naturally mated, and their offspring are not kept for milking, similar to New Zealand (Holmes *et al.*, 2002). For the CB path, it was based on calves being born when 80% of cows were 4-years old and 20% were 5-years old. For the BB and BC paths, the generation intervals correspond to those reported by Sneddon *et al.* (2016) (Table 1).

Genomic selection approach

This approach simulated the implementation of a theoretical GS-scheme (Turbo scheme: bulls selected based on parent average genomic enhanced breeding values (GEBVs) and used for breeding purposes as soon as they are sexually mature at 15 months) as proposed by Thomasen *et al.* (2014a). In this scenario, 2000 cows are selected as bull mothers according to their EBVs for the overall selection objective (VEL). Five hundred progeny bull calves from the selected cows are assumed to

Table 1. Population size, population selected, proportion selected, and selection intensities for a progeny testing selection scheme and for a genomic selection scheme for the dairy cattle population

Pathway	Population	Population selected	Proportion selected	Intensity of selection	Generation interval	Accuracy of prediction
Progeny test						
BB	150	15	0.10	1.75	6.5	0.90
BC	150	30	0.20	1.40	7.0	0.90
CB	170 450	990	0.0058	2.84	4.2	0.56
CC	500 000	495 000	0.99	0.03	4.9	0.56

Pathway	Population	Population selected	Proportion selected	Intensity of selection	Generation interval	Accuracy of prediction		
						R^2 = 40%	R^2 = 50%	R^2 = 60%
Genomic selection								
BB	500	15	0.03	2.27	2.0	0.63	0.71	0.77
BC	500	15	0.03	2.27	2.0	0.63	0.71	0.77
CB	170 450	2000	0.0117	2.61	4.2	0.56	0.56	0.56
CC	500 000	495 000	0.99	0.03	4.9	0.56	0.56	0.56

BB, bull to breed bull; BC, bull to breed cow; CB, cow to breed bull; CC, cow to breed cow; R^2, reliability

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Table 2. Genetic standard deviation (σ_g), heritability (h^2), repeatability (Rep) and genetic (below the diagonal) and phenotypic (above the diagonal) correlations among traits considered in the Valor Económico Lechero selection index

Trait	σ_g	h^2	Rep	MY	FY	PY	AFC	CI	SCS	Longevity
MY	551.62	0.290	0.510		0.81	0.94	−0.05	0.09	−0.09	−0.06
FY	21.14	0.340	0.500	0.70		0.86	−0.02	0.06	−0.06	−0.04
PY	16.45	0.300	0.500	0.90	0.83		−0.02	0.07	−0.06	−0.01
AFC[a]	7.82	0.010		−0.71	−0.29	−0.65		−0.07	0	0
CI	2.32	0.002	0.046	0.48	0.36	0.32	0		0.04	−0.08
SCS	0.39	0.120	0.320	−0.04	0.10	0.07	0	0.22		−0.07
Longevity[a]	0.48	0.050		−0.34	−0.21	−0.18	0	−0.54	−0.56	

MY, milk yield; FY, fat yield; PY, protein yield; AFC, age first calving; CI, calving interval; SCS, somatic cell score.
[a]Repeatability of age at first calving and longevity was assumed identical to heritability.

be genotyped, only 15 of them were assumed to be selected for BB and BC paths. Hence, this approach considers a proportion of bulls of 3% in the BB and BC paths and 1.19% in the CB path, respectively. This approach assumed reliabilities (R^2) of 40%, 50%, and 60%, and a two-year interval in the BB and BC paths. The assumption of this scenario are presented in Table 1.

Initially, the elite cows selected (based on their EBVs) as bull mothers are also screened (Pryce and Deatwyler, 2012) but with the goal of estimating the SNPs effects, since these cows are part of the reference population (individuals with phenotypes records and genotypes). This reference population is used to derive prediction equations to calculate GEBVs for the selection of young bulls (Hayes *et al.*, 2009).

Selection index

In the design of the selection scheme for the Chilean dairy cattle population, selection index theory (Hazel, 1943) was used to investigate the selection objective indicated by VEL.

Selection index theory

The selection index (I) is a method for predicting the selection objective (H) in which several valuable traits are selected simultaneously, such as $I = H$. These expressions are represented in the online Supplementary File according to Cameron (1997). For the selection objective investigated in this study, traits in I were the same as those included in H. Estimated genetic and phenotype parameters (heritability, repeatability, correlation, and variance) used in the selection index were from Montaldo *et al.* (2017) for MY, FY, PY, AFC, and LIC; Lembeye *et al.* (2016) for SCS and Pritchard *et al.* (2012) for longevity. These parameters are presented in Table 2. All (co)variances were formulated separately for the four pathways because of the differences in their sources of information. The formulas used to calculate elements of the matrices P and G were derived using the methodology presented by Cameron (1997). The structure of the final matrices P and G was symmetric and positive definitive.

In the selection index theory, true breeding values of traits included in H are weighed according to their economic values. However, in VEL only their relative emphases (RE) are known (Lama and Vargas, 2020); consequently, economic values were derivated based on their RE using the reverse method described by Berry (2015), so that the economic value of a trait in product with its σ_g represents the desired relative economic emphasis assigned by VEL (Table 3).

Table 3. Economic values (EV) ($) and relative emphasis (RE) for traits included in the Valor Económico Lechero selection index.

	EV[a]	RE (%)
Milk (kg)	−27.3	10
Fat (kg)	1520.7	23
Protein (kg)	2123.8	25
Age first calving (days)	1430.4	8
Calving interval (days)	−4,812.7	8
Somatic cell score (units)	− 32 276.8	9
Longevity (score)	49 862.6	17

[a]Chilean pesos.

Calculation of genetic gain

The expected correlated response in each trait was calculated using the following equation (Cameron, 1997):

$$\Delta R_j = i\frac{b'G_i}{\sqrt{b'Pb}}$$

where ΔR_j is the correlated response for the jth trait in the selection objective, G_i is the ith column of the genetic (co)variances matrix G, and i is the intensity of selection. Matrix P and row vector b as previously defined.

In the GS-scheme proposed, it was considered the aggregate breeding value (merit for all traits included in the selection objective as a single-trait). The correlated response was calculated as defined by Rendel and Robertson (1950):

$$\Delta G = \frac{\sum_{i=1}^{4}(i_i r_i)\sigma_g}{\sum_{i=1}^{4} L_i}$$

where σ_g, r_i, i_i and $L_i$are the genetic standard deviation of the aggregate breeding value (selection objective), the accuracy of selection ($\sqrt{R^2}$), selection intensity and generation interval, respectively in the ith selection pathway.

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Table 4. Correlated response (ΔG) per year from selection on the Valor Económico Lechero selection index in the Chilean dairy population from progeny testing selection scheme

	ΔG
Milk yield (kg)	42.22
Fat yield (kg)	3.51
Protein yield (kg)	2.27
Age at first calving (days)	−0.285
Calving interval (days)	−0.018
Somatic cell score (units)	−0.019
Longevity (score)	0.033

Results

Predicted responses per year in the Chilean dairy cattle population based on the proposed PT-scheme are presented in Table 4. Estimates of genetic progress were: 41.50 kg/year, 3.44 kg/year, 2.33 kg/year, −0.280 d/year, −0.017 d/year, −0.019 units/year, and 0.032 d/year for MY, FY, PY, AFC, CI, SCS, and longevity, respectively.

Table 5 shows predicted genetic gains in overall selection objectives (which is the overall genetic merit) based on the simulated PT and GS schemes. The overall genetic gain for the simulation that considered the PT-scheme was 0.194 σ_g/year, meantime those that considered GS were 0.323, 0.348 and 0.371 σ_g/year for a 40%, 50% and 60% R^2, respectively.

Discussion

The results presented in Table 4 indicate that genetic gain for MY is 25% smaller as compared with a simulation carried out in New Zealand by Sneddon *et al.* (2016), however, milk solids composition is 30–55% greater. Compared with another study under pastoral systems (Lembeye *et al.*, 2021), predicted genetic response for FY and PY agree with simulations for the once-daily milking population in New Zealand only when bulls were tested in twice-daily milking systems. In the simulation for the PT-scheme, the genetic response for milk solids is smaller in Lembeye *et al.* (2021) as compared with results shown in Table 4, and only similar for MY when udder-related type traits are included in the selection objectives. These differences result from different genetic parameters (h^2 and genetic variances) evaluated for the selected population (Chilean dairy cattle, Overo Colorado breed).

A reduction for reproduction traits in both AFC and CI is expected (−0.280 and −0.018, respectively). It is important to note that this study arbitrarily assigned an equal 8% RE for both traits because the VEL index indicated a 16% RE for reproduction traits (Lama and Vargas, 2020). In consequence, there might be differences in the RE for AFC and CI in the VEL index.

Table 5. Asymptotic annual response (ΔG) in genetic standard deviation (σ_g) per year in the Chilean dairy population based on the traditional progeny testing and an approach to genomic selection.

Scheme	ΔG (σ_g/yr)	Relative to PT (%)
PT	0.198	
GS-40% reliability	0.333	168
GS-50% reliability	0.359	181
GS-60% reliability	0.389	196

From this simulation study, we can expect a small reduction in SCS and a small increment in longevity. For longevity, the direction of the selection response agrees with Sneddon *et al.* (2016) and Lembeye *et al.* (2021), however, this finding cannot be directly compared with those studies since the genetic variance used in this simulation was measured in a score scale, while in Sneddon *et al.* (2016) and Lembeye *et al.* (2021) it was measured in days. There are no reported genetic parameters for longevity in Chilean dairy cattle, and this trait is not considered in VEL.

The results presented in this study are important because no other studies have predicted the potential genetic improvement for a proper selection objective in southern Chile. Nevertheless, theoretically, there is at least an eight-year period before genetic gains from the proposed PT-scheme (Lembeye Illanes, 2016) may be realised. The time between the scheme implementation and the realised genetic gain may be a disincentive for implementing a PT-scheme in Chile, suggesting that the current alternative is preferred since proven bulls are already selected and available with a VEL score. This is supported by Mulder *et al.* (2006) who advised that a specific selection programme is not justified when only a small amount of semen is available (as might be the case of the Chilean dairy population). Further, assuming no significant $G \times E$ between the traits of the selection objective evaluated in Chile and foreign countries, the practice of semen importation, from a large environment-specific selection programme (i.e. as from New Zealand or the United States), resulted in a greater (33%) rate of economic response compared to the implementation of a local PT selection scheme (Vargas and van Arendonk, 2004), even though the response was smaller than that achieved in the exporter country. For instance, Verdugo *et al.* (2004) reported that in Chile, selection response for yield traits was not much more than half of the response found in the United States. These reductions are likely consequences of selection schemes designed according to the semen exporting country circumstances which vary compared with importing countries (Chile, in our case). Therefore, the practice of importing frozen semen from bulls of foreign populations must be strategically used according to production and economic circumstances if farm profitability is to be maximised (López-Villalobos *et al.*, 2001). Furthermore, interactions between genotype and physical environment and between genotype and economic (milk payment and feed costs) environment must be carefully considered.

In the current calculation of the VEL index for the ranking of bulls in Chile, the imported bulls (frozen semen) are evaluated with progeny in their country of origin, and their VEL index scores are calculated through conversion (linear regression) equations (Weigel and Powell, 2000). However, this procedure is unclear since Chile does not routinely participate in INTERBULL (International Bull Evaluation Services) analyses. This advises evaluating foreign bulls with Chilean progeny to obtain their national (Chilean) EBVs, and then assess their economic value, taking as a starting point the VEL selection index. The challenge for the Chilean dairy industry is, therefore, to run annually an independent genetic evaluation across all bulls from the breeding companies currently in the market. An example of this model is NZAEL (New Zealand Animal Evaluation Limited) that produces the national evaluation of New Zealand dairy cattle independently of the breeding companies (López-Villalobos and Garrick, 2005).

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Instead of a PT- scheme, it may be advisable to implement in Chile a GS- scheme given the greater genetic gain under GS compared to the conventional PT (Table 5), mainly because of a reduced generation interval, as reported by Schaeffer (2006), Pryce *et al.* (2010) and Thomasen *et al.* (2014a). The constraint, however, is lower accuracy compared with PT because selected young bulls are not in the reference population or they are not the progeny of proven bulls (Harris and Johnson, 2010; Thomasen *et al.*, 2014b). Reference populations are mostly produced with PT bulls and they have low R^2 if they belong to a small dairy cattle population (Thomasen *et al.*, 2014b).

The results of this study suggest that cow genotyping is advised to expand a reference population (Pryce and Daetwyler, 2012). For instance, Thomasen *et al.* (2014b) reported that a 57–122% increase in R^2 resulted when 2000 simualted first-lactation cows were added to the reference population as compared to bulls only added to the reference population, indicating that the greatest profit is expected when animals are selected based on GEBVs and used when they are sexually mature. In agreement with that study, a 166–191% greater genetic response is expected under the GS-scheme compared with the PT-scheme (Table 5). This scenario necessarily requires an independent breeding organisation to produce the phenotypes for traits included in VEL and derive prediction equations to calculated GEBVs.

In conclusion, a GS scheme might be a preferred option in the implementation of a dairy selection programme in Chile. The results of this study leads one to consider this selection scheme to be more feasible for the southern Chilean dairy population, above a conventional PT scheme. However, to produce GEBVs for economically important traits, an organisation independent from breeding companies should be created to produce the phenotypes for these traits.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0022029922000504

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