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RESEARCH ARTICLE

Responses in lactose yield, lactose percentage and protein-to-protein-plus-lactose ratio from index selection in New Zealand dairy cattle

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ABSTRACT

The breeding goal of the New Zealand dairy industry is to improve the genetic capability of cows to convert pasture-based feed into farmer profit. The New Zealand dairy industry exports over 95% of milk produced and the most significant product by export volume is whole milk powder (WMP). The current selection objective, breeding worth (BW), will increase yields of protein and fat, potentially shifting milk composition further from the ideal composition for making WMP. This study aimed to investigate the correlated responses in lactose yield (LY), lactose percentage (LP) and protein-to-protein-plus-lactose ratio (P:P + L) from selection for BW, BW plus LY, BW plus LP and BW plus P:P + L. Selection for BW is predicted to have per-cow responses of 54.92 kg milk/year, 2.22 kg fat/year, 1.78 kg protein/year and 2.84 kg lactose/year. When lactose was included in the selection objective in the form of LY, LP or P:P + L, genetic responses ranged from –59.98 kg to 61.08 kg milk/year and from –2.67 kg to 3.70 kg lactose/year. The industry could reduce imported lactose requirements per tonne of WMP by 6%–11% by including lactose into the selection objective, compared with selection on BW alone.

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Introduction

The breeding goal for genetic improvement of the New Zealand dairy industry is to improve the genetic capability of the cows to convert feed into farm profit. This breeding goal is expressed as a selection objective called breeding worth (BW), which ranks the genetic superiority or inferiority of an animal expressed in dollars of net profit per 5 tonnes of dry matter consumed (NZAEL 2014).

The selection objective is calculated as the sum of the true breeding values and economic values. Selection indices are used as a predictor of a selection objective. However, there are many potential selection indices which can represent a selection objective; however, selection index theory predicts the selection index which maximises the correlation between the best selection index and selection objective (Hazel 1943).

The BW selection objective is calculated as:

$$BW = \sum_{i=1}^7 BV_i \times EV_i$$

where BV_i is the true breeding value of an animal for trait i and EV_i its corresponding economic value. Traits considered in BW are lactation yields of milk, fat and protein, mature cow live weight, somatic cell score (SCS) calculated as $\text{Log}_2(\text{somatic cell count})$, cow fertility and residual survival (NZAEL 2014). The selection index is of the same form as the selection objective using estimated breeding values.

The estimated breeding values in BW are expressed relative to a genetic base animal defined as the average cow born in 2000 (DairyNZ 2013). Correlated responses in lactose from selection on BW are not routinely calculated because, in New Zealand, lactose is currently excluded from payment systems for milk, herd testing records and genetic evaluations. The BW index was introduced in 1996 including fat, protein, milk yield, live weight and survival (Spelman & Garrick 1997). Over time, BW has been modified and built upon, with the addition of new traits of economic importance, to reach its current form including seven traits (DairyNZ 2013).

New Zealand exports dairy products representing over 95% of milk produced in New Zealand and the most significant product by export volume is whole milk powder (WMP), followed by skim milk powder (SMP). These two products represented more than 70% of dairy exports in 2013 (Fonterra 2014). The shift in focus from cheese and butter production in the 1970s and 1980s to increasing amounts of milk powders in the 1990s to present has generated market signals that have resulted in significant changes to the way in which the New Zealand dairy herd is bred, with a shifting emphasis from fat yield to protein yield as the major trait of economic importance. The inclusion of lactose yield into BW has not been undertaken because the high genetic correlation (0.98) with milk yield implies BV for lactose yield would be almost identical to BV for milk yield (Sneddon et al. 2015). However, current selection will limit the rate at which milk volume can change due to its negative economic value while increasing protein and fat yields. The consequence has been shown to reduce the WMP production potential of the New Zealand dairy industry (Sneddon et al. 2014). However, that previous study assumed lactose percentage was fixed and lactose yield responses could not be separated from responses in milk yield. A trait called protein-to-protein-plus-lactose (P:P + L), which is the ratio of protein yield to protein yield plus lactose yield, was calculated as a proxy of the capacity to produce WMP. The present study allows for a less than perfect genetic correlation between lactose yield and milk yield, and quantifies correlated responses in lactose yield, lactose percentage and P:P + L from selection for BW and modified BW indices including BW plus lactose, BW plus lactose percentage and BW plus P:P + L.

Materials and methods

Selection indices and selection objectives

Selection indices were constructed using selection theory (Hazel 1943) to investigate eight different selection objectives (Table 1). The traits included were the same as those in the

Table 1. Economic values and relative emphasis for traits in breeding worth and relative emphasis for different selection objectives investigated including selection for lactose yield, lactose percentage and protein-to-protein-plus-lactose.

Trait ^b	Selection objective ^a								
	BW		BW _{LLY} RE	BW _{HLY} RE	BW _{LLP} RE	BW _{HLP} RE	BW _{LPL} RE	BW _{MPL} RE	BW _{HPL} RE
	EV	RE							
Milk yield (kg)	-0.099	14.6	12.5	8.2	14.5	9.9	24.3	22.0	11.9
Fat yield (kg)	2.04	13.6	11.6	7.7	13.5	9.2	22.5	20.4	11.1
Protein yield (kg)	9.17	39.9	34.0	22.5	39.7	27.2			
Live weight (kg)	-1.66	13.1	11.2	7.4	13.1	9.0	-21.8	19.8	10.7
Fertility (%)	7.18	5.1	4.3	2.9	5.0	3.5	8.5	7.7	4.2
SCS	-38.37	8.7	7.4	4.9	8.7	5.9	14.5	13.1	7.1
Residual survival (days)	0.135	5.0	4.3	2.8	5.0	3.4	8.3	7.6	4.1
Lactose yield (kg)			14.7	43.6					
Lactose percentage					0.5	31.9			
P:P + L							0.1	9.4	50.9

^aBW, breeding worth; BW_{LLY}, BW with additional low relative economic weighting for lactose yield (EV = \$2.04); BW_{HLY}, BW with additional high relative economic weighting for lactose yield (EV = \$9.17); BW_{LLP}, BW with additional low relative economic weighting for lactose percentage (EV = \$9.17); BW_{HLP}, BW with additional high relative economic weighting for lactose percentage (EV = \$9.17); BW_{LPL}, BW with additional low relative economic weighting on P:P + L with protein yield excluded from the index (EV = \$9.17); BW_{MPL}, BW with additional medium relative economic weighting on P:P + L (EV = \$9.17) with protein yield excluded from the index; BW_{HPL}, BW with additional high relative economic weighting for P:P + L (EV = \$9.17) with protein yield excluded from the index; EV, economic values; RE, relative emphasis.

^bSCS, somatic cell score (log₂ somatic cell count); P:P + L, protein-to-protein-plus-lactose ratio.

BW selection index plus various measures of lactose. The base scenario was selection on BW with the economic values as published in the February 2014 economic value update (NZAEL 2014). BW_{HLY} is BW with LY included at the value of PY, BW_{LLY} is BW with LY included at the value of FY, BW_{LLP} is BW with LP included at the same value as PY, BW_{HLP} is BW with LP included at 100 times the value of PY, BW_{LPL} is BW with P:P + L included at a negative value equal to the value of PY and PY excluded from the objective, BW_{MPL} is BW with P:P + L included at a negative value equal to 100 times the value of PY and PY excluded from the index and BW_{HPL} BW with P:P + L included at a negative value equal to 1000 times the value of PY and PY excluded from the index. All economic values and relative emphases are shown in Table 1. Relative emphasis on each trait was calculated by multiplying the absolute economic value by genetic standard deviation of each trait; this was then summed and each trait was expressed as a proportion of the sum of all traits. The economic value for LY in BW_{HLY} was chosen as equal to the economic value for PY as this has the highest positive economic value of the production traits in BW. The economic value for LY in BW_{LLY} was chosen as equal to the economic value for FY as this has the lowest positive economic value of the production traits in BW. The economic values for LP and P:P + L were set equal to the economic value for PY in BW_{LLP} and BW_{LPL} to determine the effect of placing equal economic value on these traits as PY. The economic value for LP in BW_{HLP} was determined so as to be equal in emphasis to PY in BW. The economic value for P:P + L in BW_{HPL} was determined as the point at which a positive genetic response for P:P + L was achieved.

The indices were of the form

$$I = b_1x_1 + b_2x_2 + \dots + b_mx_m = \mathbf{b}'\mathbf{x}$$

where x_i is an observation on the i th trait and b_i is the selection index coefficient (or weighting) for that trait. In vector notation $\mathbf{b}' = [b_1, b_2, \dots, b_m]$ and $\mathbf{x}' = [x_1, x_2, \dots, x_m]$.

The selection objectives were of the form:

$$H = a_1g_1 + a_2g_2 + \dots + a_n g_n = \mathbf{a}'\mathbf{g}$$

where g_i is the true breeding value of the i th trait and a_i is the economic value of the corresponding trait. In vector notation $\mathbf{a}' = [a_1, a_2, \dots, a_n]$ and $\mathbf{g}' = [g_1, g_2, \dots, g_n]$.

The vector \mathbf{b} was calculated from solving the equation:

$$\mathbf{b} = \mathbf{P}^{-1}\mathbf{G}\mathbf{a}$$

where \mathbf{P} is the $n \times n$ phenotypic variance-covariance matrix of the traits (n) used in the selection index and \mathbf{G} is the $n \times m$ genetic covariance matrix between traits in the selection index (n) and traits in the aggregate genotype (m). For all scenarios traits included in the selection index were the same as those included in the selection objective.

Calculation of genetic gain

Correlated responses (R) to selection were calculated using selection index theory (Cameron 1997). This was done individually for each of the eight investigated scenarios using the equation:

$$R_j = \frac{\mathbf{b}'\mathbf{C}_j}{\sqrt{\mathbf{b}'\mathbf{P}\mathbf{b}}}$$

where R_j is the R for the j th trait and \mathbf{C}_j is the j th column in matrix \mathbf{C} , \mathbf{C} is a matrix that includes the genetic covariances between all traits included in the selection index, selection objective and other traits of interest (LY, LP, P:P + L and PY) if they were not in either index. Matrices \mathbf{P} and \mathbf{C} were derived from parameters shown in Table 2, with assumed values calculated as the average proportion of the known correlations between known traits. Genetic and phenotypic correlations are in Table 2. Genetic parameters were taken from several sources (Spelman & Garrick 1997; Pryce & Harris 2006; Sneddon et al. 2016), and these matrices were checked to ensure they were positive definite and those that were not underwent bending using the procedure of Jorjani et al. (2003). After bending, the final variance and covariance matrices were inspected and, in general, these values were found to be similar to the originals.

Variances and co-variances for each of the individual pathways were formulated using the methodology of Pretto et al. (2012). Due to the differences in sources of information, the formulae were as follows.

Cow pathways

Elements in matrix \mathbf{P} :

$$P_{ii} = \left[r + \frac{1-r}{n} \right] \times \sigma_{pii}^2$$

$$P_{ij} = \frac{\sigma_{pij} + (n - 1) \times \sigma_{gij}}{n}$$

Elements in matrix **C**:

$$C_{ii} = \sigma_{gii}^2$$

$$C_{ij} = \sigma_{gij}$$

Bull pathways

Elements in matrix **P**:

$$P_{ii} = \frac{[r + (1 - r/n)] + (p - 1)k \times h^2}{p} \times \sigma_{pii}^2$$

$$P_{ij} = \frac{(\sigma_{pij} + (n - 1) \times \sigma_{gij}/n) + k \times \sigma_{gij}}{p}$$

Elements in matrix **C**:

$$C_{ii} = a \times \sigma_{gii}^2$$

$$C_{ij} = a \times \sigma_{gij}$$

where:

σ_{pii}^2 = phenotypic variance of trait i ;

σ_{gii}^2 = genetic variance of trait i ;

σ_{pij} = phenotypic covariance between traits i and j ;

σ_{gij} = genetic covariance between traits i and j ;

n = number of phenotypic records per animal (own performance in cow pathways, performance of daughters in bull pathways);

h^2 = the heritability of the trait;

r = repeatability of the trait;

p = number of animals in progeny group;

k = relationship among animals in progeny groups (half-sibs 0.25); and

a = relationship among animals in progeny groups and animals to evaluate (bull to daughter = 0.5).

Breeding scheme

The four pathways of selection (Rendel & Robertson 1950) were used to calculate an overall industry rate of genetic gain. The assumptions used in the four pathways are presented in Table 3, specifically for cows to breed cows (CC), cows to breed bulls (CB), bulls to breed cows (BC) and bulls to breed bulls (BB). Selection intensities carried by pathways; all cows were available for the CC pathway; CB was calculated using all cows in lactations 3 and 4; 440 bulls available for progeny test for BC, BB with the top 10% selected for BC and top 2% for BB. For the calculation of selection intensity 99.85% of animals in CC, 0.25% (2640 cows, six cows to produce one bull for progeny test) of animals in CB, 10% (44 bulls)

of animals in BC, 2.05% (9 bulls) of animals in BB were available for selection, respectively, based on Lopez-Villalobos & Garrick (2005). Generation intervals were 5.6, 4.2, 7 and 6.5 years for CC, CB, BC and BB, respectively. These were based on the age structure of the national herd (LIC & DairyNZ 2014) for the CC pathway. For CB it was based on calves being born when 80% of cows were 4 years old and 20% were 5 years old. The BC and BB generation intervals were based on time required to gain progeny records on 85 daughters. Number of records per animal was based on Spelman & Garrick (1997) with two records on cows and 85 records on daughters.

Industry production of milk components and dairy products

The genetic responses were used in the industry model described in Sneddon et al. (2014) to generate industry and per-cow milk production responses after 10 years of selection, which did account for overlapping generations and assumed 100% use of artificial insemination. The base cow was assumed to have a genetic potential consistent with phenotypic production of 4480 kg of milk, 222 kg of fat, 169 kg of protein, 210 kg of lactose and 460 kg of live weight (LIC & DairyNZ 2013). The calculations used in this article estimate changes to the industry production of milk, fat, protein and lactose yields, and live weight over 10 years based on genetic gains for milk, fat, protein and lactose yields, and live weight. The industry is constrained by total area of 1.677 million ha (LIC & DairyNZ 2013) and feed availability (12,090 kg DM intake/ha), leading to decreases in stocking rate as feed demand per cow increases, energy requirements were calculated from milk, fat and protein yields, and live weight. The estimated industry milk production from 10 years of selection for each selection objective was then used in the Moorepark processing sector model (Geary et al. 2010) to estimate the potential milk product yields. The model of Geary et al. (2010) is a mass balance milk processing model, which can simulate varying product portfolios. In this study, 60% of milk was used to produce WMP, 23.5% of milk was used for SMP, 14% of milk for cheese, 0.5% for butter and 2.0% for casein. The product mix was used as an approximation of the Fonterra 2012–2013 product yields (Fonterra 2012a,b,c, 2013).

Values of WMP, SMP, cheese, butter, lactose, BMP and casein were obtained from GlobalDairy Trade (2015) historic results (averaged from 15 May 2013 to 19 May 2015). The value of WP was obtained from the European Commission (2015) historic milk product values (average 19 May 2013 to 17 May 2015) and converted to US dollars using NZForex (2015) historic exchange rate values for each day there was a WP value. Total industry income was calculated by multiplying the yield of each dairy product by its value.

Results

Genetic responses are in Table 4 for each of the scenarios. Under selection for BW the predicted genetic response was MY 54.92 kg/year, FY 2.22 kg/year, PY 1.78 kg/year and LY 2.84 kg/year. Live weight was predicted to increase at 1.04 kg/year, residual survival was predicted to increase at 0.077 days/year, with a small decrease in fertility, SCS, LP and P:P + L. With LY included in the selection objective with the same economic weighting as PY (BW_{HLY}), the rate of gain in MY and LY increased to 61.08 kg/year and 3.70 kg/year, respectively. Fat yield and PY decreased to 1.71 kg/year and 1.77 kg/year,

Table 2. Genetic (below diagonal) and phenotypic (above diagonal) correlations among traits used in investigated selection indices for breeding worth, and breeding worth including either lactose yield, lactose percentage and protein-to-protein-plus-lactose ratio before matrix bending.

Traits ^a	σ_g	h^2	r	Milk yield	Fat yield	Protein yield	Live weight	Fertility	SCS	Survival	Lactose yield	Lactose percentage	P:P + L
Milk yield	227.81 ^c	0.23 ^c	0.60 ^b		0.73 ^c	0.91 ^c	0.25 ^e	-0.002 ^e	-0.13 ^e	0	0.99 ^c	-0.08 ^c	-0.26 ^c
Fat yield	10.27 ^c	0.29 ^e	0.60 ^b	0.54 ^c		0.82 ^c	0.24 ^e	0.02 ^e	-0.09 ^e	0	0.73 ^c	-0.09 ^c	0.13 ^c
Protein yield	6.72 ^c	0.29 ^e	0.60 ^b	0.86 ^c	0.69 ^c		0.30 ^e	0.02 ^e	-0.10 ^e	0	0.91 ^c	-0.08 ^c	0.07 ^c
Live weight	12.24 ^e	0.39 ^e	0.65 ^b	0.28 ^e	0.33 ^e	0.36 ^e		0.05 ^e	0.04 ^e	0	0.25 ^d	0.00004 ^d	-0.00004 ^d
Fertility	1.10 ^e	0.03 ^e	0.05 ^e	-0.15 ^e	-0.06 ^e	-0.05 ^e	0.03 ^e		-0.02 ^e	0	0.00005 ^d	-0.00005 ^d	0.00005 ^d
SCS	0.35 ^e	0.18 ^e	0.30 ^e	0.04 ^e	0.12 ^e	0.06 ^e	-0.01 ^e	-0.10 ^e		0	-0.09 ^d	-0.16 ^d	0.13 ^d
Residual survival	57.40 ^e	0.07 ^e	0.11 ^e	0	0	0	0	0	0		0 ^d	0 ^d	0 ^d
Lactose yield	13.02 ^c	0.50 ^c	0.67 ^c	0.98 ^c	0.39 ^c	0.82 ^c	0.23 ^d	-0.14 ^d	-0.20 ^d	0 ^d		0.07 ^c	-0.32 ^c
Lactose percentage	0.08 ^c	0.64 ^c	0.64 ^c	-0.16 ^c	-0.19 ^c	-0.29 ^c	0.00004 ^d	-0.0001 ^d	-0.10 ^d	0 ^d	0.03 ^c		-0.39 ^c
P:P + L	0.01 ^c	0.43 ^c	0.60 ^c	-0.57 ^c	0.01 ^c	-0.13 ^c	-0.00004 ^d	0.0001 ^d	0.12 ^d	0 ^d	-0.66 ^c	-0.45 ^c	

Notes: σ_g , genetic standard deviation; h^2 , heritability; r , repeatability.

^aSCS, somatic cell score (log₂ somatic cell count); P:P + L, protein-to-protein-plus-lactose ratio.

^bSpelman & Garrick (1997).

^cSneddon et al. (2016).

^dAssumed values.

^ePryce & Harris (2006).

Table 3. Assumptions pertaining to the four pathways of selection, including starting population size, proportion selected, intensity of selection, generation interval, number of records and number of progeny (in sire proving scheme).

Pathway ^a	Population	Proportion selected	Intensity of selection (<i>i</i>)	Generation interval (years)	Number of records	Number of progeny
CC ^b	4,800,000	0.998	0.02	5.6	2	0
CB ^b	1,056,000	0.003	3.033	4.2	2	0
BC ^c	440	0.10	1.755	7.0	4	85
BB ^c	440	0.02	2.420	6.5	4	85

^aBB, bulls to breed bulls; BC, bulls to breed cows; CB, cows to breed bulls; CC, cows to breed cows.

^bRecords on the animal itself.

^cRecords on progeny.

respectively. Live weight gains increased to 1.17 kg/year. Fertility, SCS, LP and P:P + L all had small negative responses. Residual survival had a decrease in the response rate to 0.02 days/year.

The response in MY was less than the BW_{HLY} scenario when the economic value of LY was reduced to equal that of FY (BW_{LLY}), but was still greater than BW alone. Fat yield and LY responses were both intermediate between BW and BW_{HLY}, with PY having a greater response than under the BW_{HLY} scenario. Fertility, SCS, LP and P:P + L all had small negative responses and residual survival had small positive responses.

Under selection for LP at the same economic value as PY (BW_{LLP}), responses in all traits were similar to those under BW alone; however, there were slightly higher responses in MY and LY than under BW. When this value was increased 100 fold (BW_{HLP}), however, response rates changed dramatically, with responses in MY, FY and PY more than halved. Lactose percentage was predicted to have a small increase. This was the largest predicted genetic response per year for LP of all scenarios.

When investigating the P:P + L scenarios, PY was removed as an economic trait in the index to avoid double counting. In the scenarios when P:P + L was equal to the negative

Table 4. Correlated responses per year in traits for the current New Zealand dairy industry selection objective (breeding worth) and alternative selection objectives including either lactose yield, lactose percentage or the ratio of protein-to-protein-plus-lactose.

Trait ^b	Selection objective ^a							
	BW	BW _{LLY}	BW _{HLY}	BW _{LLP}	BW _{HLP}	BW _{LPL}	BW _{MPL}	BW _{HPL}
Milk yield (kg)	54.92	59.90	61.08	54.96	21.84	-59.98	-49.46	32.33
Fat yield (kg)	2.22	2.03	1.71	2.22	0.80	-0.95	-0.93	0.15
Protein yield (kg)	1.78	1.84	1.77	1.78	0.59	-1.36	-1.31	0.29
Live weight (kg)	1.04	1.14	1.17	1.04	0.65	-1.35	-1.48	-0.16
Fertility (%)	-0.0256	-0.0328	-0.0381	-0.0257	-0.0190	0.0343	0.0370	0.0021
SCS (units)	-0.0027	-0.0060	-0.0090	-0.0028	-0.0145	-0.0154	-0.0206	-0.0117
Residual survival (days)	0.077	0.052	0.023	0.077	0.064	0.150	0.175	0.044
Lactose yield (kg)	2.84	3.37	3.70	2.85	2.07	-2.55	-2.67	0.03
Lactose percentage (%)	-0.0099	-0.0072	-0.0038	-0.0096	0.0142	0.0030	0.0020	-0.0025
P:P + L (units)	-0.0004	-0.0004	-0.0004	-0.0004	0.0002	0.0016	0.0004	-0.0030

^aBW, breeding worth; BW_{LLY}, BW with additional low relative economic weighting for LY; BW_{HLY}, BW with additional high relative economic weighting for LY; BW_{LLP}, BW with additional low relative economic weighting for LP; BW_{HLP}, BW with additional high relative economic weighting for LP; BW_{LPL}, BW with additional low relative economic weighting on P:P + L with PY excluded from the index; BW_{MPL}, BW with additional medium relative economic weighting on P:P + L with PY excluded from the index; BW_{HPL}, BW with additional is high relative economic weighting for P:P + L with PY excluded from the index.

^bSCS, somatic cell score (log₂ somatic cell count); P:P + L, protein-to-protein-plus-lactose ratio.

equivalent of PY (BW_{LPL}) or 100 times PY's (BW_{MPL}) original value, the genetic responses became negative for all yield traits (MY, FY, PY and LY). When a very high emphasis was placed upon P:P + L (1000 times the original value of protein) (BW_{HPL}) the genetic responses were positive rates of gain; however, these were just over half those in the BW scenario for MY and were around 10% of the gains for FY, PY and LY. All scenarios selecting on P:P + L led to a decrease in live weight and a positive response in fertility. The BW_{HPL} scenario led to the most negative genetic response in P:P + L; however, this was still small at -0.0027 units per year.

The relative emphases of each trait are in Table 1 for each selection objective. Under selection on BW, PY has the greatest economic emphasis, followed by MY and FY. Under selection for BW_{HLY} the emphasis on all traits decreased relative to LY, which was the most emphasised trait. For BW_{LLY} the relative emphasis was similar to BW with LY slightly higher than MY or FY. Similarly, when selecting for BW_{LLP} , relative emphasis on traits was similar compared with the BW scenario and LP accounted for a very small amount of the total emphasis. Under selection for BW_{HLP} , the LP emphasis was similar to levels for PY in BW, decreasing the relative emphasis on all other traits. The selection objectives that included P:P + L and excluded PY (BW_{LPL}), resulted in a relative emphasis that was lower than that of LP in BW_{LLP} , while all other traits had increased relative emphasis. Under BW_{MPL} the relative emphasis on P:P + L was around a similar level to that of SCS in BW, while all other traits had greater emphasis than in BW. In the final scenario with BW_{HPL} , the relative emphasis was half of the total and decreased all other traits to levels around 3% below their emphasis in BW.

Changes in cow numbers, milk production per cow and industry milk production after 10 years of selection are in Table 5. The base year had 4.8 million cows, producing on average 3943 kg of milk, 197 kg of fat, 150 kg of protein and 185 kg of lactose, for a total production of 18.9 billion kg of milk, 943 million kg of fat, 720 million kg of protein and 889 million kg of lactose. Under selection for BW, MY per cow increased by 12.2%, FY increased by 9.6%, PY increased by 10.7%, lactose increased by 13.2% and total cow numbers decreased by 4.7%. Industry production increased by 7.0%, 4.7% 5.3% and 7.9% for MY, FY, PY and LY, respectively, without accounting for increases in the survivability in these cows.

The greatest reductions in cow numbers occurred under selection for BW, BW_{LLP} and BW_{LLY} , the greatest increase in cow numbers occurred under selection for BW_{LPL} . Milk yield per cow increased the most under selection for BW_{HLY} , while the greatest reduction occurred under selection for BW_{LPL} . The greatest increase in FY per cow was estimated to occur under selection for either BW or BW_{LLY} , while selection for BW_{LPL} or BW_{MPL} reduced FY. Protein yield per cow increased the most under selection for BW_{HLY} and experienced the reductions when selecting for either BW_{LPL} or BW_{MPL} . The greatest increase in LY per cow was estimated to occur under selection for BW_{HLY} followed by BW_{LLY} with selection for either BW_{LPL} or BW_{MPL} reducing LY production. When considered as the overall industry, milk, protein and lactose production was greatest under selection for BW_{HLY} with fat production greatest under selection for BW and BW_{LLP} . Industry production of all components was least under selection for BW_{LPL} and BW_{MPL} .

The highest PP (3.96%) was achieved under selection for BW_{LPL} ; this also produced the highest FP (5.33%), whereas the highest LP (4.87%) was achieved under selection for

Table 5. Estimated milk, fat, protein and lactose production per cow, across the industry (thousands of tonnes) and the size of the required cow population based on the genetic gains derived after 10 years of selection for the current selection objective or alternative selection objectives including lactose yield, percentage and the ratio of protein to protein-plus-lactose.

Trait	Selection objective								
	Base year	BW	BW _{LLY}	BW _{HLV}	BW _{LLP}	BW _{HLP}	BW _{LPL}	BW _{MPL}	BW _{HPL}
Number of cows	4,800,000	4,575,294	4,575,974	4,587,058	4,575,208	4,678,336	4,871,803	4,859,567	4,700,449
Yield per cow									
Milk (kg)	3,943	4,425	4,458	4,466	4,425	4,202	3,650	3,721	4,273
Fat (kg)	197	216	215	213	216	207	195	195	202
Protein (kg)	150	166	166	166	166	158	144	145	156
Lactose (kg)	185	210	213	216	210	205	173	173	191
Fat (%)	4.99	4.88	4.82	4.76	4.88	4.92	5.33	5.24	4.73
Protein (%)	3.81	3.74	3.72	3.71	3.74	3.75	3.96	3.89	3.64
Lactose (%)	4.70	4.74	4.78	4.82	4.74	4.87	4.75	4.64	4.46
Industry yield (millions of kg)									
Milk	18925	20245	20402	20488	20246	19657	17781	18081	20083
Fat	944	988	983	975	988	966	949	947	950
Protein	720	758	760	760	758	737	704	704	731
Lactose	889	959	976	989	960	957	845	838	897

Notes: BW, breeding worth; BW_{LLY}, BW with additional low relative economic weighting for lactose yield; BW_{HLV}, BW with additional high relative economic weighting for lactose yield; BW_{LLP}, BW with additional low relative economic weighting for lactose percentage; BW_{HLP}, BW with additional high relative economic weighting for lactose percentage; BW_{LPL}, BW with additional low relative economic weighting on P:P + L with protein yield excluded from the index; BW_{MPL}, BW with additional medium relative economic weighting on P:P + L with protein yield excluded from the index; BW_{HPL}, BW with additional is high relative economic weighting for P:P + L with protein yield excluded from the index.

BW_{HLP} . The highest P:P + L (0.456) was achieved under selection for BW_{MPL} and the lowest (closer to the ideal) was achieved under selection for BW_{HLY} .

Milk product yields and the levels of lactose deficit are in Table 6. When using 60% of milk for WMP, a total of 214,200 tonnes of lactose was required to fill the deficit. Whole milk powder production was greatest under selection for BW_{HLY} , while WMP production was lower than the base year for BW_{LPL} and BW_{MPL} . The greatest reduction in lactose deficit was modelled under selection for BW_{HLP} followed by BW_{HLY} with all selection indices including P:P + L increasing the lactose deficit. Skim milk powder production was greatest under selection for BW_{HLY} , with least SMP produced when selecting for BW_{LPL} or BW_{MPL} ; the same was seen for cheese, casein and WP. Butter production was greatest under selection for BW_{LPL} or BW_{MPL} with least butter produced when selecting for BW_{HPL} ; the same trend was seen for BMP.

The most efficient scenario for use of imported lactose (measured as kg of imported lactose/tonne of WMP) was BW_{HLY} at 103.7 kg of lactose per tonne of WMP produced, a reduction of 21.8% relative to the base year (126.3 kg), followed by BW_{HLP} at 103.8 kg of lactose per tonne of WMP, a 21.6% reduction relative to base year. The least efficient scenario was BW_{MPL} at 140.3 kg of lactose per tonne of WMP, a 10.0% increase in the deficit relative to the base year.

The greatest total industry income was achieved under selection for BW_{LLY} (5.26% increase over base), followed by selection for BW_{HLY} (5.23% increase). Selection for BW_{LPL} or BW_{MPL} reduced the total industry income by 1.68% and 1.83%, respectively.

Discussion

The genetic responses to selection on BW simulated in this study were higher than the industry reported values (54.9 kg MY compared to 44 kg MY) for 2012 (most recent publication of genetic gains), but closer to published gains prior to 2012 (Bryant 2012). The study by Spelman & Garrick (1997) on the then inclusion of live weight into the early BW showed that genetic gains in PY would be greater than FY and that MY would increase at 29 kg per year. The inclusion of LY in the selection objective increased the genetic gains in MY, as could be expected given the high genetic correlations between MY and LY (0.95–0.99; Johnson et al. 2000; Miglior et al. 2007; Sneddon et al. 2012). Gains in MY and LY were not equal, however. Lactose percentage increased from 4.70% to 4.82% under the BW_{HLY} scenario, indicating that it may be possible to increase LP through selection on LY while restricting MY. Intense selection on LP was also found to increase LP, showing the possibility to alter LP through genetic selection. Genetic gain estimations for FY and PY were similar in this study to those reported for industry for the dairy season 2011–2012 (Bryant 2012) (2.22 vs 2.22 kg/year and 1.82 vs 1.78 kg/year for FY and PY in the New Zealand industry and the present study, respectively). Genetic gains in fertility, SCS, live weight and residual survival were lower than industry reports; this may be explained by the bending procedures used in the selection index, as well as different genetic and phenotypic variances used in this study due to differences in selected populations.

Selection responses in all production traits to the two selection objectives that included P:P + L with lower emphasis (BW_{LPL} and BW_{MPL}) were negative. This suggests that the weighting was not sufficient (relative emphasis of 0.1% and 9.4% for P:P + L in each

Table 6. Industry production of milk products (thousands of tonnes) and industry income (millions of \$US) based on genetic gains derived after 10 years of selection for current selection objective or alternative selection objectives including lactose yield, percentage and the ratio of protein to protein-plus-lactose.

Product ^b	Base year	Selection objective ^a							
		BW	BW _{LLY}	BW _{HLY}	BW _{LLP}	BW _{HLP}	BW _{LPL}	BW _{MPL}	BW _{HPL}
WMP	1695.7	1781.9	1787.3	1791.5	1781.9	1733.9	1650.6	1649.4	1721.7
SMP	469.7	495.5	497.9	499.7	495.6	483.2	454.8	454.8	478.1
Cheese	331.5	348.3	349.3	350.1	348.3	338.9	322.9	322.6	336.4
Butter	413.9	429.8	422.2	411.0	429.8	424.8	436.2	436.4	410.0
BMP	49.8	51.7	50.9	49.7	51.7	51.9	54.3	53.1	46.9
Casein	11.8	12.4	12.5	12.5	12.4	12.1	11.5	11.5	12.0
WP	150.9	171.9	174.4	176.4	171.9	170.6	151.7	151.2	162.1
Total industry income (\$US millions)	11,039	11,632	11,652	11,648	11,632	11,382	10,856	10,841	11,165
Lactose deficit (thousands of tonnes)	214.2	204.4	194.2	185.8	204.4	180.1	227.7	231.4	222.6
Change in lactose deficit (%)	–	–2.18%	–8.71%	–11.85%	–3.91%	–13.46%	5.88%	0.25%	3.55%

^aBW, breeding worth; BW_{LLY}, BW with additional low relative economic weighting for lactose yield; BW_{HLY}, BW with additional high relative economic weighting for lactose yield; BW_{LLP}, BW with additional low relative economic weighting for lactose percentage; BW_{HLP}, BW with additional high relative economic weighting for lactose percentage; BW_{LPL}, BW with additional low relative economic weighting on P:P + L with protein yield excluded from the index; BW_{MPL}, BW with additional medium relative economic weighting on P:P + L with protein yield excluded from the index; BW_{HPL}, BW with additional high relative economic weighting for P:P + L with protein yield excluded from the index.

^bWMP, whole milk powder; SMP, skim milk powder; WP, whey powder; BMP, butter milk powder.

scenario, respectively) to overcome the negative weighting on MY (relative emphasis of 24.3% and 22.0% in each scenario, respectively) in these objectives. As a result MY, FY, PY and LY all experienced negative genetic gains. These scenarios did, however, result in positive gains in fertility and were the only selection objectives to achieve this.

The base cow in this simulation had similar milk production to the industry average animal in the 2012–2013 dairy season (LIC & DairyNZ 2014). Selection on BW_{LPL} or BW_{MPL} produced a cow with production similar to the 2003–2004 dairy season (LIC & DairyNZ 2014), indicating that these selection objectives would reverse 10 years of genetic gain. Limiting land area and feed available may reduce the potential increases in industry production, but under selection for BW the total milk production increased 7.0% while stock numbers reduced 4.7%, indicating that BW would produce a more efficient cow in terms of milk product production. This was not the same for the objectives BW_{LPL} and BW_{MPL} which increased stock numbers and decreased milk production, indicating that a less efficient cow (for milk production) was created.

Changes in LP were found in most scenarios to be smaller than changes in FP or PP, which was consistent with the study of Vos & Groen (1998). That may be a result of the smaller genetic variance in LP than FP and PP. High direct selection pressure (BW_{HLP} or BW_{MPL} or BW_{HPL}) was required to alter LP faster than FP or PP, which were not directly selected upon.

A previous study (Sneddon et al. 2014) into the potential outcomes of breeding for BW was based on the assumption that LP would remain constant under selection for BW, but this study indicates that LP could increase over time. The report by Sneddon et al. (2014) showed a 14% increase in the lactose deficit after 10 years of selection for BW; however, this study indicated that there may actually be a 2.19% reduction in lactose deficit. These differences can be associated with differences between an assumed correlated response and a correlated response from selection index theory. The lactose deficit can be further reduced under selection for BW_{HLY} or BW_{HLP} in a situation where 60% of milk is being used for WMP production.

Selection on the ratio of P:P + L did not have the anticipated outcome with the genetic gains increasing the ratio over time. Including P:P + L in the selection objective increased the amount of additional lactose required to produce a tonne of WMP relative to the base year, even though total milk and WMP production was reduced. This is possibly due to differences in the heritabilities between the numerator (0.29) and denominators (0.29 and 0.50) in the ratio (Gunsett 1984). Due to the very small genetic variance in the trait (0.00011), high emphasis is required to cause a shift in the ratio and removes relative selection emphasis from the other traits in the index. Studies have shown that differential selection on the components on ratio results in a greater response than selection on the ratio itself (Zetouni et al. 2015).

Selection on BW increased the efficiency of WMP production by reducing the requirement for imported lactose per tonne of WMP (114 kg/tonne vs 126 kg/tonne in the base year). The value of this cannot be completely evaluated, but would amount to a saving of between \$10 and \$18 per tonne of WMP or between \$9 and \$33 million over the industry. This would be dependent on the value of lactose, which has ranged from a high price in 2012–2013 of (\$1967/tonne) to lower prices in 2014–2015 of (\$1076/tonne) (GlobalDairy Trade 2015). Using selection for BW_{HLY} and BW_{HLP} , the savings could be more than doubled to \$30 million or \$70 million per year over the entire industry. Including LY at

the economic value of FY would save between \$30 million and \$57 million, and this scenario also kept the other traits very similar to the gains that would be achieved using just BW.

When evaluated on a total industry income basis, the scenario which gave the greatest gross return was BW_{LLY} (5.26% higher relative to base), because butter production was increased relative to the base. Whereas in BW_{HLY}, butter production decreased relative to BW, causing a decrease in total income. Savings in lactose costs have to be greater than losses in income from reductions in other product yields. In the BW_{HLP} scenario, the largest decrease in lactose deficit, the reductions in total WMP yield is greater than the savings in lactose leading to a total increase in income of 3.0% relative to base year, lower than BW alone which is a 5.1% increase compared to the base year. Selection for BW_{LPL} and BW_{MPL} decreased total product yields relative to the base year and accordingly decreased total income by 1.7% and 1.8%, respectively. High selection on P:P + L led to a small increase in total income (1.1%). These results indicate that inclusion of LY at a lower emphasis (such as BW_{LLY}) could be advantageous in increasing farmer incomes compared with selection on BW alone.

Conclusion

This study is the first to show that the selection objective in New Zealand is both increasing the efficiency of milk production and also reducing the requirement for imported lactose in WMP production. This is also the first study to evaluate the effect of including lactose into the selection objective on the milk product portfolio and lactose requirements in the New Zealand dairy industry. The industry could reduce imported lactose requirements per tonne of WMP by 6%–11% by including lactose into the selection objective. If imported lactose becomes a significant issue for the industry (due to market pressures), the most efficient means to reduce external lactose requirements, according to this study, would be to include LY with an economic value similar to FY into the selection objective, compared with selection on BW alone.

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