



Heritabilities and genetic and phenotypic correlations for milk production and fertility traits of spring-calved once-daily or twice-daily milking cows in New Zealand

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ABSTRACT

The objectives of this study were to estimate the genetic and phenotypic correlations and heritabilities for milk production and fertility traits in spring-calved once-daily (OAD) milking cows for the whole season in New Zealand and compare those estimates with twice-daily (TAD) milking cows. Data used in the study consisted of 69,252 first parity cows from the calving seasons 2015–2016 to 2017–2018 in 113 OAD and 531 TAD milking herds. Heritability estimates for production and fertility traits were obtained through single-trait animal models, and estimates of genetic and phenotypic correlations were obtained through bivariate animal models. Heritability estimates of production traits varied from 0.26 to 0.61 in OAD and from 0.13 to 0.63 in TAD. Heritability estimates for fertility traits were low in both OAD and TAD milking cow populations, and estimates were consistent (OAD: 0.01 to 0.10 and TAD: 0.01 to 0.08) across milking regimens. Estimates of phenotypic and genetic correlations among production traits were consistent across populations. In both populations, phenotypic correlations between milk production and fertility traits were close to zero, and most of the genetic correlations were antagonistic. In OAD milking cows, genetic correlations of milk and lactose yields with the start of mating to conception, 6-wk in-calf, not-in-calf, and 6-wk calving rate were close to zero. Interval from first service to conception was negatively genetically correlated with milk and lactose yields in OAD milking cows. Protein percentage was positively genetically correlated with 3-wk and 6-wk submission, 3-wk in-calf, 6-wk in-calf, first service to conception, 3-wk calving, and 6-wk calving rate in the TAD milking cow population, but these correlations were low in the OAD milking cow population. Further

studies are needed to understand the relationship of protein percentage and fertility traits in the OAD milking system. The phenotypic correlations between fertility traits were similar in OAD and TAD milking populations. Genetic correlations between fertility traits were strong (≥ 0.70) in cows milked TAD, but genetic correlations varied from weak to strong in cows milked OAD. Further research is required to evaluate the interaction between genotype by milking regimen for fertility traits in terms of sire selection in the OAD milking cow population.

Key words: fertility, milk composition, once-daily milking, genetic correlation

INTRODUCTION

Genetic and phenotypic correlations between milk production and fertility measures of dairy cows have been well studied in seasonal (Grosshans et al., 1997; Pryce et al., 1997; Evans et al., 2002; Haile-Mariam et al., 2003) and nonseasonal dairy production systems (Campos et al., 1994; Castillo-Juarez et al., 2000; Tiezzi et al., 2012). The main conclusion from the cited studies is that genetic correlations between milk production and fertility traits are antagonistic, indicating that selection for increased milk production results in genetically less fertile cows. Consequently, most dairy cattle breeding programs have incorporated fertility in their selection indices (Miglior et al., 2005). In New Zealand, fertility has been included in the Breeding Worth index since 2001 (Harris and Montgomerie, 2001).

The New Zealand dairy production system is pasture-based and has a seasonally concentrated calving pattern with fixed calendar dates for the start of mating and calving in a year. The proportion of cows that conceive in the first 6 wk of the mating season (6-wk in-calf rate; **PR42**) is one of the key reproductive indicators in seasonal calving herds. This indicator is an outcome of both 3-wk submission (**SR21**) and conception to first service (**PRFS**; Xu and Burton, 2003). In New

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Zealand, national averages for SR21, PRFS, and PR42 have improved from 78.5, 50.1, and 63.4% in 2008–2009 to 81.3, 52.7, and 67.7% in the 2020–2021 production seasons, respectively (LIC and DairyNZ, 2021). This improvement in reproductive performance of the national herd is likely to be caused by both managerial factors and increases in fertility breeding values (Pryce et al., 2014).

Since the late 1990s, some farmers have adopted once-daily (**OAD**) milking for the whole lactation in New Zealand (Davis et al., 1999). For the production season 2015–2016, about 55% of herd-tested farms were milked twice daily (**TAD**) for the entire lactation whereas about 9% of herds were milked OAD for the entire lactation, and the remainder of farms practiced a mixture of TAD and OAD milking (Edwards 2018). Studies in New Zealand reported that cows milked OAD had improved energy balance in early lactation (Kay et al., 2013; Phyn et al., 2014), and cows milked OAD for the entire lactation had better reproductive performance than cows milked TAD (Jayawardana et al., 2022). Lembeye et al. (2016) reported genetic and phenotypic correlations between milk yields and milk composition traits in OAD milking cows in New Zealand. But so far, the genetic and phenotypic associations between production and fertility traits have not been calculated for the OAD milking cow population.

In New Zealand, Harris and Pryce (2004) reported significant phenotypic associations and low genetic correlations between milk protein percentage and both SR21 and the probability of having a calf born to artificial breeding (**AB**). Positive phenotypic and genetic associations between milk composition and fertility traits have been reported in seasonal and split-calving Australian herds (Fahey et al., 2017; Haile-Mariam and Pryce, 2017; Morton et al., 2018) and in spring-calving herds in Ireland (Buckley et al., 2003; Carty et al., 2020). Morton et al. (2018) reported that the association between milk protein concentration and fertility is influenced by both genetic and nongenetic components, and cow reproductive performance can be maximized by improving genetic and nongenetic management strategies. To provide strategies for farmers to improve reproductive performance, it is important to understand the genetic and phenotypic correlations between milk composition and fertility traits in dairy cows milked OAD or TAD.

Lembeye et al. (2021) reported the genetic correlations for same milk production traits expressed across the OAD and TAD milking frequency were strong but lower than unity. It is of interest to investigate the genetic correlations of milk production and fertility traits in OAD and TAD milking cow populations because common sires are used in both milking environments.

The genetic correlations between milk production and fertility traits could be different in OAD compared with TAD milking populations because the extent of negative energy balance in early lactation is reduced for cows milked OAD rather than TAD. Therefore, the objective of this study was (1) to estimate the genetic and phenotypic correlations and heritabilities for milk production and fertility traits in cows milked OAD for the whole season in New Zealand, and (2) to compare the estimated genetic and phenotypic correlations for cows milked OAD with those for cows milked TAD.

MATERIALS AND METHODS

The data used in this study was collected by farmers as part of normal farming practice and retrospectively extracted and analyzed. Therefore, animal ethics approval was not required for this study.

Initial Data Set

Herd-test milk yields, calving, mating and pregnancy diagnosis dates, lactation yields, and pedigree information of first parity spring-calved dairy cows in 3 calving seasons from 2015 to 2016 to 2017–2018 in New Zealand were extracted from the Livestock Improvement Corporation database. Herd milking regimen classification and editing of milk production and fertility data were described in Jayawardana et al. (2023). Herds were included in this study if they had at least 50 cows in a herd, were herd tested at least 4 times per lactation in each calving season, had pregnancy diagnosis (**PD**) test results for at least 80% of cows that calved in the 12-mo period, and had early-aged PD results for at least 80% of cows in a herd. The resulting data set consisted of 488,946 spring-calving first-lactation dairy cows in 2,421 herds.

Herd Classification

A herd-test day milking regimen was used to classify the herds into OAD or TAD milking categories. If more than 90% of the tested cows in a herd at a herd-testing date were milked OAD, then the herd was classified as being OAD at that test date. Similarly, TAD milking herds were identified as those where more than 90% of the cows were milked TAD in the herd-test date. If all the herd tests were classified as either OAD or TAD from 2015 to 2016 to 2017–2018 calving seasons, then the herd was identified as OAD or TAD throughout the period, respectively. All other herds were excluded. Using the GPS Visualizer (Schneider, 2012), peer TAD milking herds were selected within a radius of 20 km from an OAD milking herd. In some cases, there were

no TAD milking herds within 20 km from an OAD milking herd. These OAD milking herds ($n = 8$) were excluded from the data set. There were 114 OAD and 554 TAD herds comprised of 17,134 of OAD milking and 86,233 of TAD milking cows.

Breed and Heterosis Information

Pedigree information with breed composition (expressed in sixteenths) was used to classify the cows into 3 breed groups: Holstein Friesian (**F**), Jersey (**J**), and a crossbreed of Holstein Friesian and Jersey (**F** × **J**). All cows in the data set had 100% known breed composition and no more than 12.5% of any breed other than the F or J. Herds that did not have F, J, and crossbred F × J cows were excluded ($n = 3$ TAD herds). Coefficients of individual and maternal heterosis were calculated for each cow using the following equation (Dickerson, 1973):

$$h_{F \times J} = \alpha_F^S \alpha_J^D + \alpha_J^S \alpha_F^D,$$

where the calculation of individual heterosis coefficient for progeny α_F^S and α_J^S are breed proportions of F and J in the sire, respectively, and α_J^D and α_F^D are breed proportions of J and F in the dam, respectively. The calculation of maternal heterosis coefficient dam α_F^S and α_J^S are breed proportions of F and J in the maternal grand-sire, and α_J^D and α_F^D are breed proportions of J and F in the maternal granddam, respectively.

Milk Production Traits

Lactation records of milk (**MY**), fat (**FY**), protein (**PY**), and lactose (**LY**) yields (kg) with DIM ranging from 150 to 305 d were included. Cows with MY greater than 12,500 kg or less than 800 kg, or FY, PY, and LY greater than 600 kg or less than 30 kg, were excluded ($n = 3,264$). Percentages of fat (**FP**) and protein (**PP**) and lactose (**LP**) were calculated for each lactation record as the ratio between FY, PY, or LY and MY multiplied by 100.

Fertility Traits

Calving dates between June 1 and December 31 in each calving season were retained. Cows with age at first calving that was greater than 900 d were excluded. The mating start and end dates for each herd were obtained from the Livestock Improvement Corporation database. The mating start date of a herd was defined as the first of 2 consecutive days, both with at least one

mating recorded, where at least 3 of the next 6 d also have mating records. The mating end date of the herd was defined as either (1) the last recorded mating date on or before the 21st wk of the mating period or, (2) the last date with 2 conceptions followed by at least 30 d with no conceptions on or before the 21st wk of the mating period or, (3) the last date with one conception on or before the 21st wk of the mating period followed by at least 30 d with no conceptions and had at least one conception on each of 2 or more other days in the 6 preceding days. Herds with the start of the mating before September 15 in each spring-calving season were excluded ($n = 1$ in OAD and $n = 21$ in TAD). Mating date records outside the herd's breeding season were excluded from the calculation of fertility traits due to uncertainty of those records ($n = 264$). Cows that were missing both a PD and all herd tests after the end of the mating period were considered to have left the herd before the end of mating and were discarded from the data set ($n = 2,164$).

Conception dates were determined from the results of transrectal ultrasound or rectal palpation PD. Pregnancy testing results where the fetal age was estimated and where cows were tested on or between 35 and 122 d from conception were used. Conception dates were calculated as the date of PD minus the estimated fetal age for cows with a pregnancy status of pregnant ($n = 47,742$). Conception dates were also calculated for cows without recorded PD results but which calved in the subsequent season as the date of subsequent calving minus 282 d ($n = 1,514$). The detailed description for the calculation of conception date, 3-wk in-calf (**PR21**), PR42, and not in-calf (**NIC**) for cows in all parities was described in Figure 3 in Jayawardana et al. (2023).

Table 1 defines the fertility traits and the criteria for trait calculations in the present study. Cows with no recorded AB inseminations ($n = 2,653$) were allocated the end date of the AB period in the herd as a penalized first service date. The end of the AB period was identified in each herd as the date of the last AB insemination that was not followed by another AB insemination within 7 d. Penalized conception dates for cows that did not conceive ($n = 8,093$) were allocated as the mating end date in each herd plus 21 d (Johnston and Bunter, 1996; Grosshans et al., 1997). The planned start of calving date for subsequent calving year was derived for each herd by adding 282 d to the herd's mating start date in each calving year.

The final data set used for genetic parameters estimation was comprised of 10,709 first parity cows from 113 OAD herds and 58,543 first parity cows from 531 TAD herds. The distribution of cows by breed in OAD and TAD herds was: 1,362 (12.7%) F; 2,791 (26.1%)

Table 1. Description of fertility traits and criteria for calculation

Abbreviation	Description of traits and criteria for calculation
Production traits	
MY (kg)	305-d milk production
FY (kg)	305-d fat production
PY (kg)	305-d protein production
LY (kg)	305-d lactose production
FP (%)	Fat percentage, kg fat per kg milk
PP (%)	Protein percentage, kg protein per kg milk
LP (%)	Lactose percentage, kg lactose per kg milk
Fertility traits	
SMFS ¹ (d)	Interval from the start of mating to the first service
SMCO ² (d)	Interval from the start of mating to conception
FSCO ² (d)	Interval from the first service to conception
CFS ¹ (d)	Interval from calving to first service
CIN ³ (d)	Interval between 2 consecutive calvings
SR21	Presentation (1) or nonpresentation (0) for mating in the first 21 d from the start of the mating date
SR42	Presentation (1) or nonpresentation (0) for mating in the first 42 d from the start of the mating date
PR21	Conceived (1) or not conceived (0) in the first 21 d from start of mating date
PR42	Conceived (1) or not conceived (0) in the first 42 d from start of mating date
PRFS	Conceived (1) or not conceived (0) to first service
NIC	Conceived (0) or not conceived (1) by end of the mating period
CR21 ⁴	Calved within the first 21 d of the planned start of calving date herd in the subsequent season (1) or calved after the first 21 d from the planned start of calving in the subsequent season (0)
CR42 ⁴	Calved within the first 42 d of the planned start of calving date herd in the subsequent season (1) or calved after the first 42 d from the planned start of calving in the subsequent season (0)

¹Intervals for cows with no recorded artificial breeding (AB) were ended at the end of the AB period of herd in each calving season.

²Intervals for cows that did not conceive were ended at the herd's end of the mating date plus 21 d.

³Intervals for cows with positive pregnancy diagnosis results and without subsequent calving dates were calculated by estimating a calving date using conception date plus 282 d.

⁴Cows that did not calve in the subsequent season were treated as missing variables.

J; and 6,556 (61.2%) F × J cows in OAD and 25,297 (43.2%) F; 4,351 (7.4%) J; and 28,895 (49.4%) F × J cows in TAD.

Estimation of Genetic Parameters

Statistical data analysis was carried out using the ASReml version 4.1 software package (Gilmour et al., 2015). Variance components and heritability were estimated using a single-trait animal model, and bivariate animal models were used separately to estimate the (co)variance components, genetic, and phenotypic correlations. Contemporary groups were defined for cows in the same herd and calving year as herd-year. The single-trait animal model was represented as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e},$$

where \mathbf{y} is the vector of observations for each production and fertility traits in Table 1; \mathbf{b} is the vector of fixed effects, \mathbf{a} is the vector of additive genetic effects, \mathbf{e} is the vector of random residual effects. \mathbf{X} and \mathbf{Z} are

incidence matrices relating to the records of fixed and animal additive genetic effects, respectively.

The fixed effects were contemporary group of herd-year; the regression coefficients related to the linear effect of the proportion of F in the cow and dam, respectively (proportion of J for cow and dam was not included in the model due to the linear dependencies); the regression coefficients related to the linear effect individual and maternal heterosis coefficients, respectively; the regression coefficients related to the linear and quadratic effects of deviation of calving date from median calving date of the herd within the season, and the regression coefficients related to linear and quadratic effects of deviation of age at first calving from median calving in months. Logit scale was used to estimate the variance components related to binary fertility traits in Table 1 with the random residual variance of $\pi^2/3 = 3.2899$.

The expected values (E) of the variables were assumed as $E(\mathbf{y}) = \mathbf{Xb}$, $E(\mathbf{a}) = 0$, and $E(\mathbf{e}) = 0$. The residuals were assumed to be independently distributed and $\text{var}(\mathbf{y}) = \mathbf{ZAZ}'\mathbf{A}\sigma_a^2 + \mathbf{R}$, $\text{var}(\mathbf{a}) = \mathbf{A}\sigma_a^2$, and $\text{var}(\mathbf{e})$

$= \mathbf{I}\sigma_e^2 = \mathbf{R}$; where σ_a^2 was the animal additive genetic variance, σ_e^2 was the random residual variance, \mathbf{A} was the numerator relationship matrix between all the cows, and \mathbf{I} was the identity matrix that corresponds to the number of cows with records.

Heritability (h^2) for each trait was calculated using the following ratio (Falconer and Mackay, 1996):

$$h^2 = \sigma_a^2 / \sigma_p^2,$$

where σ_p^2 was the phenotypic variance, similar to $\sigma_p^2 = \sigma_a^2 + \sigma_e^2$.

In matrix notation, the bivariate model was represented as follows:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix},$$

where \mathbf{y}_1 and \mathbf{y}_2 are the vectors of phenotypic measures for 2 traits; \mathbf{X}_1 , \mathbf{X}_2 , \mathbf{Z}_1 , and \mathbf{Z}_2 were design matrices relating the fixed and animal additive genetic effects related to the \mathbf{y}_1 and \mathbf{y}_2 phenotypes, respectively; \mathbf{b}_1 and \mathbf{b}_2 were the vectors of fixed effects of herd-year, the regression coefficients related to the linear effect of the proportion of F in the cow and dam, respectively, the regression coefficients related to the linear effect of individual and maternal heterosis coefficients, respectively, the regression coefficients related to the linear and quadratic effects of deviation of calving date from median calving date of the herd in the given calving season and the regression coefficient related to the linear effect of deviation of age at first calving from median calving in months; \mathbf{a}_1 and \mathbf{a}_2 were the vectors of random effects of animal for each trait; and \mathbf{e}_1 and \mathbf{e}_2 were vectors of residual errors.

The expected values of the variables were assumed $E(\mathbf{y}_1) = \mathbf{X}_1\mathbf{b}_1$; $E(\mathbf{y}_2) = \mathbf{X}_2\mathbf{b}_2$; $E(\mathbf{a}) = 0$ and $E(\mathbf{e}) = 0$. The residuals were assumed to be normally distributed with zero mean and following co(variance) structure:

$$\text{var} \begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{a1}^2 & \mathbf{A}\sigma_{a12} & 0 & 0 \\ \mathbf{A}\sigma_{a12} & \mathbf{A}\sigma_{a2}^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_{e1}^2 & \mathbf{I}\sigma_{e12} \\ 0 & 0 & \mathbf{I}\sigma_{e12} & \mathbf{I}\sigma_{e2}^2 \end{bmatrix},$$

where σ_{a1}^2 was the additive genetic variance of the trait 1; σ_{a2}^2 was the additive genetic variance of trait 2; and σ_{a12} was the additive genetic covariance between both traits. \mathbf{I} was an identity matrix of size 10,709 and 58,543 for OAD and TAD populations; σ_{e1}^2 was the residual

variance for trait 1; σ_{e2}^2 was the residual variance of trait 2; and σ_{e12} was the residual covariance between both traits.

Genetic correlations (r_g) were estimated as (Falconer and Mackay, 1996):

$$r_g = \frac{\sigma_{a12}}{\sigma_{a1} \times \sigma_{a2}},$$

where σ_{a1} and σ_{a2} were genetic additive standard deviation for trait 1 and trait 2, respectively.

Phenotypic correlations (r_p) were estimated as (Falconer and Mackay, 1996):

$$r_p = \frac{\sigma_{P12}}{\sigma_{P1} \times \sigma_{P2}},$$

where σ_{P12} was phenotypic covariance between phenotypic trait 1 and trait 2; σ_{P1} and σ_{P2} were phenotypic standard deviation for trait 1 and trait 2, respectively.

RESULTS

Reproductive Performance

Descriptive statistics of production and fertility traits by milking frequency are shown in Table 2. First parity cows milked TAD had greater ($P < 0.001$) yields of milk, fat, protein, and lactose compared with cows milked OAD, but with lower ($P < 0.001$) percentages of fat and protein and a higher ($P < 0.001$) percentage of lactose. Cows milked OAD had improved reproductive performance compared with cows milked TAD with shorter ($P < 0.001$) intervals from the start of mating to first service (**SMFS**: 1.4 d), start of mating to conception (**SMCO**: 6.6 d), first service to conception (**FSCO**: 5.4 d), and consecutive calving interval (**CIN**: 3.5 d). Higher proportions ($P < 0.001$) of cows that were milked OAD were mated (6%) and conceived (11%) in the first 3 wk of the mating period compared with cows milked TAD. Also, PRFS was higher ($P < 0.001$) in OAD than TAD. Consequently, reproductive performance as measured by PR42 (higher, $P < 0.001$), and NIC (lower, $P < 0.001$) was superior in cows milked OAD. The proportion of cows calved by 3 wk (**CR21**) and calved by 6 wk (**CR42**) were also greater ($P < 0.001$) in cows milked OAD compared with cows milked TAD.

Variance Components and Heritability

Estimates of variance components and heritabilities for production and fertility traits of first parity dairy

Table 2. Descriptive statistics of milk production and fertility traits by milking regimen in first lactating dairy cows in New Zealand

Trait	Once-daily milking			Twice-daily milking		
	Mean	SD	CV	Mean	SD	CV
Production¹						
MY	2456 ^b	631	26	4158 ^a	1,057	25
FY	133 ^b	33	25	197 ^a	48	24
PY	102 ^b	26	25	160 ^a	40	25
LY	123 ^b	32	26	212 ^a	55	26
FP	5.5 ^a	0.7	12.4	4.8 ^b	0.7	14.5
PP	4.2 ^a	0.3	6.9	3.9 ^b	0.3	7.5
LP	5.0 ^b	0.2	3.6	5.1 ^a	0.2	3.5
Fertility²						
SMFS	12.2 ^b	10.8	88.4	13.6 ^a	13.7	100.6
SMCO	25.9 ^b	22.5	87.0	32.5 ^a	26.7	82.0
FSCO	13.9 ^b	20.9	149.8	19.4 ^a	25.1	129.5
CFS	85.8 ^a	20.1	23.5	86.4 ^a	20.6	23.8
CIN	375.0 ^b	23.4	6.2	378.5 ^a	25.3	6.7
SR21	0.89 ^a	0.31	35.3	0.83 ^b	0.38	45.7
SR42	0.95 ^a	0.22	22.7	0.93 ^a	0.25	26.4
PR21	0.59 ^a	0.49	84.0	0.48 ^b	0.50	104.2
PR42	0.79 ^a	0.41	51.6	0.69 ^b	0.46	66.9
PRFS	0.65 ^a	0.48	72.7	0.57 ^b	0.49	86.0
NIC	0.09 ^b	0.28	323.5	0.13 ^a	0.34	259.8
CR21	0.67 ^a	0.47	69.6	0.60 ^b	0.49	82.3
CR42	0.89 ^a	0.32	35.9	0.82 ^b	0.38	46.5

^{a,b}Means with different superscripts within the same row are significantly different ($P < 0.001$). Models were fitted for each trait with fixed effects of milking regimen, the proportions of Holstein Friesian in cow and dam, respectively, the coefficients of individual and maternal heterosis, respectively. The deviation of calving date from median calving date of the herd within the season (linear and quadratic effects) and the deviation of age at first calving from median calving in months (linear and quadratic effects) were fitted as covariates in the models. Herd-year was fitted as a random effect.

¹MY = milk yield (kg); FY = fat yield (kg); PY = protein yield (kg); LY = lactose yield (kg); FP = fat percentage; PP = protein percentage; LP = lactose percentage.

²SMFS = start of mating to first service (d); SMCO = start of mating to conception (d); FSCO = first service to conception (d); CFS = calving to the first service (d); CIN = consecutive calving interval (d); SR21 = cow inseminated in the first 3 wk from the start of mating; SR42 = cow inseminated in the first 6 wk from the start of mating; PR21 = cow conceived in the first 3 wk from the start of mating; PR42 = cow conceived in the first 6 wk from the start of mating; PRFS = cow conceived to first service; NIC = cow not in-calf at end of the breeding season; CR21 = cow calved in the first 3 wk from the planned start of the calving; CR42 = cow calved in the first 6 wk from the planned start of the calving.

cows milked OAD and TAD populations are presented in Table 3. Heritability estimates for yields (MY, FY, PY, and LY) in the OAD population were greater than in the TAD population. Heritability estimates of milk composition traits were similar in cows milked either OAD or TAD. Heritabilities of FP and PP were more than twice as large as estimates for the respective yield traits (FY and PY) in both milking populations. The estimates of heritability for LP were similar in both milking populations and were much lower than the heritability estimates for FP and PP.

Heritability estimates of fertility traits were lower than the heritability estimates for production traits in both milking populations. Heritability estimates for fertility traits ranged from 0.01 to 0.10 in OAD and from 0.01 to 0.08 in the TAD milking population. The highest heritability estimate was for SR21 and 6-wk submission (**SR42**; 0.1 and 0.08, respectively) in OAD

and TAD milking populations, respectively. The heritability estimate for PRFS was lowest (0.01) in both milking populations. Overall, heritability estimates for fertility traits were similar between OAD and TAD milking populations.

Genetic and phenotypic correlations between yield, composition, and fertility traits for OAD and TAD milking cow populations are shown in Table 4 and Table 5, respectively.

Correlations Between the Production Traits

Milk yield was strongly positively genetically correlated with both PY and LY (≥ 0.81) in both milking populations. Genetic correlations of FY with MY, PY, and LY were low to moderate in the TAD milking population (+0.29 to +0.51), but were strong (≥ 0.71) in the OAD milking population. Genetic and pheno-

Table 3. Estimates of variances and heritabilities with standard errors for production and fertility traits of the first parity cows milked once daily (OAD) and twice daily (TAD) in New Zealand

Trait	OAD milking					TAD milking				
	Variance					Variance				
	Residual	Genetic	Total	Heritability	SE	Residual	Genetic	Total	Heritability	SE
Production¹										
MY	148,671	77,622	226,293	0.34	0.04	344,268	103,557	447,825	0.23	0.02
FY	486.6	166.9	653.5	0.26	0.04	805.5	182.2	987.6	0.18	0.02
PY	273.7	102.2	375.9	0.27	0.04	499.8	75.7	575.5	0.13	0.01
LY	399.7	216.7	616.4	0.35	0.04	938.0	273.3	1,211.2	0.23	0.02
FP	0.14	0.17	0.31	0.56	0.05	0.11	0.18	0.28	0.63	0.02
PP	0.02	0.03	0.05	0.61	0.05	0.02	0.03	0.05	0.59	0.03
LP	0.02	0.01	0.03	0.29	0.04	0.02	0.01	0.025	0.30	0.02
Fertility²										
SMFS	104.0	2.4	106.4	0.02	0.01	145.9	4.20	150.1	0.03	0.01
SMCO	676.0	21.2	697.2	0.03	0.02	917.2	37.3	954.5	0.04	0.01
FSCO	412.3	7.9	420.2	0.02	0.01	576.7	9.5	586.2	0.02	<0.01
CFS	104.0	2.4	106.4	0.02	0.01	145.9	4.2	150.1	0.03	<0.01
CIN	309.5	8.9	318.4	0.03	0.01	394.7	8.4	403.1	0.02	<0.01
SR21	3.29	0.35	3.64	0.10	0.02	3.29	0.23	3.52	0.07	0.01
SR42	3.29	0.28	3.57	0.08	0.04	3.29	0.29	3.58	0.08	0.02
PR21	3.29	0.12	3.41	0.04	0.01	3.29	0.10	3.39	0.03	0.01
PR42	3.29	0.13	3.42	0.04	0.02	3.29	0.13	3.42	0.04	0.01
PRFS	3.29	0.05	3.34	0.01	0.01	3.29	0.05	3.34	0.01	<0.01
NIC	3.29	0.23	3.52	0.07	0.03	3.29	0.16	3.45	0.05	0.01
CR21	3.29	0.11	3.40	0.03	0.02	3.29	0.09	3.38	0.03	0.01
CR42	3.29	0.04	3.33	0.01	0.03	3.29	0.12	3.41	0.03	0.01

¹MY = milk yield (kg); FY = fat yield (kg); PY = protein yield (kg); LY = lactose yield (kg); FP = fat percentage; PP = protein percentage; LP = lactose percentage.

²SMFS = start of mating to first service (d); SMCO = start of mating to conception; FSCO = first service to conception (d); CFS = calving to the first service (d); CIN = consecutive calving interval (d); SR21 = cow inseminated in the first 3 wk from the start of mating; SR42 = cow inseminated in the first 6 wk from the start of mating; PR21 = cow conceived in the first 3 wk from the start of mating; PR42 = cow conceived in the first 6 wk from the start of mating; PRFS = cow conceived to first service; NIC = cow not in-calf at end of the breeding season; CR21 = cow calved in the first 3 wk from the planned start of the calving; CR42 = cow calved in the first 6 wk from the planned start of the calving.

Table 4. Genetic (below the diagonal with standard errors in parentheses) and phenotypic (above the diagonal) correlations between milk production and fertility traits in once-daily (OAD) milking cows¹

Trait ²	MY	FY	PY	LY	FP	PP	LP	SMFS	SMCO	FSCO	CFS	CIN	SR21	SR42	PR21	PR42	PRFS	NIC	CR21	CR42
MY	0.85																			
FY	0.71 (0.04)	0.95 0.90																		
PY	0.92 (0.01)	0.84 (0.03)	0.95 (0.01)																	
LY	0.99 (0.01)	0.71 (0.04)	0.92 (0.01)	0.99 (0.01)																
FP	-0.50 (0.06)	0.25 (0.08)	-0.23 (0.08)	-0.39 (0.06)	0.95 (0.06)															
PP	-0.40 (0.07)	0.15 (0.08)	-0.01 (0.08)	-0.39 (0.07)	0.76 (0.03)	0.57 (0.08)														
LP	0.26 (0.09)	0.25 (0.09)	0.31 (0.09)	0.39 (0.08)	-0.06 (0.08)	0.01 (0.08)														
SMFS	0.42 (0.18)	0.36 (0.18)	0.43 (0.18)	0.38 (0.18)	-0.02 (0.18)	-0.12 (0.19)														
SMCO	0.08 (0.18)	0.19 (0.18)	0.14 (0.18)	0.07 (0.18)	0.14 (0.16)	0.12 (0.16)	0.42 (0.26)													
FSCO	-0.19 (0.22)	0.01 (0.22)	-0.09 (0.22)	-0.17 (0.21)	0.23 (0.21)	0.29 (0.21)	-0.02 (0.35)	0.96 (0.04)												
CFS	0.42 (0.18)	0.36 (0.19)	0.43 (0.19)	0.38 (0.18)	-0.02 (0.18)	-0.12 (0.18)	-0.11 (0.19)	0.42 (0.26)	-0.02 (0.35)											
CIN	0.21 (0.19)	0.23 (0.19)	0.20 (0.19)	0.23 (0.19)	-0.001 (0.18)	-0.10 (0.17)	0.08 (0.19)	0.88 (0.12)	0.99 (0.04)	0.96 (0.12)										
SR21	-0.53 (0.14)	-0.39 (0.14)	-0.51 (0.14)	-0.52 (0.14)	0.16 (0.14)	0.26 (0.15)	-0.04 (0.16)	-0.99 (0.01)	-0.67 (0.18)	-0.34 (0.27)	-0.34 (0.01)	-0.99 (0.17)	-0.74 (0.23)	0.71 (0.23)	0.23 (0.18)	0.23 (0.21)	-0.06 (0.17)	-0.10 (0.28)	0.30 (0.18)	0.19 (0.16)
SR42	-0.39 (0.23)	-0.42 (0.24)	-0.41 (0.23)	-0.36 (0.23)	-0.03 (0.23)	0.06 (0.23)	-0.02 (0.24)	-0.98 (0.32)	-0.52 (0.43)	0.11 (0.25)	0.11 (0.25)	-0.98 (0.05)	-0.74 (0.17)	0.71 (0.30)	0.18 (0.30)	0.21 (0.30)	-0.02 (0.38)	-0.10 (0.34)	0.18 (0.18)	0.16 (0.16)
PR21	-0.25 (0.18)	-0.30 (0.18)	-0.27 (0.18)	-0.30 (0.17)	-0.04 (0.17)	0.05 (0.16)	-0.19 (0.17)	-0.70 (0.25)	-0.93 (0.11)	-0.80 (0.43)	-0.70 (0.25)	-0.97 (0.05)	-0.97 (0.17)	0.75 (0.30)	0.96 (0.04)	0.60 (0.60)	0.44 (0.44)	-0.34 (0.34)	0.82 (0.58)	0.47 (0.82)
PR42	-0.07 (0.20)	-0.22 (0.21)	-0.13 (0.21)	-0.08 (0.20)	-0.18 (0.19)	-0.16 (0.19)	0.05 (0.20)	-0.14 (0.32)	-0.99 (0.01)	-0.92 (0.04)	-0.14 (0.32)	-0.94 (0.06)	-0.94 (0.02)	0.75 (0.30)	0.96 (0.04)	0.60 (0.60)	0.44 (0.44)	-0.34 (0.34)	0.82 (0.58)	0.47 (0.82)
PRFS	-0.16 (0.36)	-0.17 (0.37)	-0.21 (0.37)	-0.20 (0.36)	0.06 (0.32)	-0.08 (0.33)	-0.03 (0.33)	-0.02 (0.47)	-0.84 (0.09)	-0.94 (0.06)	-0.94 (0.06)	-0.94 (0.06)	-0.94 (0.06)	0.75 (0.30)	0.96 (0.04)	0.60 (0.60)	0.44 (0.44)	-0.34 (0.34)	0.82 (0.58)	0.47 (0.82)
NIC	0.06 (0.20)	0.21 (0.20)	0.13 (0.20)	0.03 (0.19)	0.16 (0.18)	0.15 (0.18)	-0.30 (0.30)	0.08 (0.33)	0.89 (0.09)	0.51 (0.47)	0.08 (0.33)	0.08 (0.33)	0.79 (0.17)	0.79 (0.23)	0.62 (0.21)	0.23 (0.21)	-0.46 (0.50)	-0.10 (0.32)	0.30 (0.39)	0.19 (0.16)
CR21	-0.55 (0.24)	-0.52 (0.24)	-0.54 (0.24)	-0.63 (0.22)	0.11 (0.23)	0.17 (0.23)	-0.60 (0.22)	-0.73 (0.30)	-0.99 (0.01)	-0.86 (0.12)	-0.73 (0.30)	-0.99 (0.01)	-0.99 (0.01)	0.51 (0.43)	0.85 (0.09)	0.94 (0.04)	-0.46 (0.16)	-0.32 (0.39)	0.30 (0.39)	0.19 (0.16)
CR42	-0.06 (0.16)	-0.02 (0.16)	0.01 (0.19)	-0.05 (0.16)	-0.01 (0.16)	0.02 (0.19)	-0.28 (0.19)	-0.71 (0.30)	-0.98 (0.01)	-0.91 (0.12)	-0.71 (0.30)	-0.71 (0.30)	-0.71 (0.30)	0.85 (0.45)	0.30 (0.71)	0.85 (0.09)	0.85 (0.09)	0.85 (0.09)	0.85 (0.09)	0.85 (0.09)

¹Standard errors for all phenotypic correlation estimates were ≤ 0.01 . All estimates were significantly different from zero and nonsignificant or nonconverged estimates were not represented.

²MY = milk yield (kg); FY = fat yield (kg); PY = protein yield (kg); LY = lactose yield (kg); FP = fat percentage; PP = protein percentage; LP = lactose percentage; SMFS = start of mating to first service (d); SMCO = start of mating to conception; FSCO = first service to conception; CFS = calving to the first service; CIN = consecutive calving interval; SR21 = cow inseminated in the first 3 wk from the start of mating; SR42 = cow inseminated in the first 6 wk from the start of mating; PR21 = cow conceived in the first 3 wk from the start of mating; PR42 = cow conceived in the first 6 wk from the start of mating; PRFS = cow conceived to first service; NIC = cow not in-calf at end of the breeding season; CR21 = cow calved in the first 3 wk from the planned start of the calving; CR42 = cow calved in the first 6 wk from the planned start of the calving.

Table 5. Genetic (below the diagonal with standard errors in parentheses) and phenotypic (above the diagonal) correlations between milk production and fertility traits in twice-daily (TAD) milking cows¹

Trait ²	MY	FY	PY	LY	FP	PP	LP	SMFS	SMCO	FSCO	CFS	CIN	SR21	SR42	PR21	PR42	PRFS	NIC	CR21	CR42	
MY	0.74																				
FY	0.29 (0.05)	0.82																			
PY	0.81 (0.01)	0.51 (0.04)	0.93																		
LY	0.98 (0.01)	0.29 (0.05)	0.79 (0.02)	0.98																	
FP	-0.65 (0.03)	0.53 (0.05)	-0.33 (0.05)	0.73	0.35																
PP	-0.70 (0.02)	0.15 (0.04)	-0.16 (0.05)	-0.69 (0.03)	0.07	0.60															
LP	-0.11 (0.05)	-0.03 (0.05)	-0.13 (0.06)	0.13 (0.05)	0.05	-0.01															
SMFS	0.26 (0.09)	0.18 (0.09)	0.22 (0.09)	0.23 (0.09)	0.17	-0.17	0.001														
SMCO	0.24 (0.08)	0.13 (0.09)	0.17 (0.09)	0.20 (0.08)	-0.10	0.08	0.08	0.89													
FSCO	0.21 (0.11)	0.12 (0.10)	0.11 (0.10)	0.16 (0.10)	-0.06	0.09	0.11	0.71	0.98												
CFS	0.26 (0.09)	0.18 (0.09)	0.22 (0.09)	0.23 (0.09)	-0.17	0.20	0.17	0.89	0.01	0.71											
CIN	0.27 (0.10)	0.18 (0.10)	0.29 (0.10)	0.25 (0.10)	-0.10	0.09	0.08	0.83	0.04	0.95	0.83										
SR21	-0.21 (0.08)	-0.18 (0.08)	-0.16 (0.09)	-0.19 (0.08)	0.10	0.22	0.17	-0.99	0.01	0.01	0.07	-0.80									
SR42	-0.17 (0.09)	-0.19 (0.10)	-0.14 (0.10)	-0.14 (0.10)	0.09	0.16	0.25	-0.98	0.01	0.10	0.03	0.06	0.98								
PR21	-0.28 (0.09)	-0.18 (0.09)	-0.25 (0.09)	-0.24 (0.09)	0.11	0.24	0.16	-0.93	0.04	0.12	0.02	0.08	0.82	0.91							
PR42	-0.28 (0.08)	-0.21 (0.09)	-0.23 (0.09)	-0.23 (0.08)	0.06	0.22	0.13	-0.89	0.01	0.03	0.04	0.25	0.87	0.88	0.97						
PRFS	-0.35 (0.12)	-0.20 (0.13)	-0.30 (0.13)	-0.30 (0.13)	0.08	0.22	0.14	-0.77	0.01	0.01	0.05	0.01	0.05	0.81	0.81	0.85					
NIC	0.25 (0.10)	0.08 (0.11)	0.12 (0.11)	0.20 (0.10)	-0.16	0.35	-0.23	0.84	0.97	0.97	0.84	0.85	-0.82	0.81	0.81	0.85					
CR21	-0.26 (0.12)	-0.10 (0.13)	-0.27 (0.13)	-0.22 (0.12)	0.15	0.22	0.11	-0.77	0.02	0.03	0.06	0.06	0.06	0.79	0.84	0.92	-0.99				
CR42	-0.27 (0.13)	-0.23 (0.14)	-0.30 (0.14)	-0.24 (0.13)	0.12	0.20	0.10	-0.88	0.01	0.04	0.09	-0.99	-0.88	0.86	0.93	0.97	0.73	-0.88			
																			0.95		
																				0.08	
																					0.05

¹Standard errors for all phenotypic correlation estimates were ≤ 0.01 . All estimates were significantly different from zero.²MY = milk yield (kg); FY = fat yield (kg); PY = protein yield (kg); LY = lactose yield (kg); FP = fat percentage; PP = protein percentage; LP = lactose percentage; SMFS = start of mating to first service (d); SMCO = start of mating to conception; FSCO = first service to conception; CFS = calving to the first service; CIN = consecutive calving interval; SR21 = cow inseminated in the first 3 wk from the start of mating; SR42 = cow inseminated in the first 6 wk from the start of mating; PR21 = cow conceived in the first 3 wk from the start of mating; PR42 = cow conceived in the first 6 wk from the start of mating; PRFS = cow conceived to first service; NIC = cow not in-calf at end of the breeding season; CR21 = cow calved in the first 3 wk from the planned start of the calving; CR42 = cow calved in the first 6 wk from the planned start of the calving.

typic correlations between MY and FP or PP were moderately negative in both milking populations. The genetic and phenotypic correlations between MY and LP were negative (-0.11) and close to zero (0.01) in the TAD milking population, but these correlations were moderately positive in the OAD milking population. The genetic correlation between FY and FP was moderately positive, but this estimate was stronger in the TAD milking population than in the OAD milking population. The genetic correlation between LY and LP was weak to moderately positive and was stronger in the OAD milking population than the TAD milking population. Estimations of genetic and phenotypic correlations between MY and LY were close to one in both milking populations.

In both milking populations, genetic and phenotypic correlations of MY, PY, LY with FP and PP had the opposite sign (negative) compared with the correlations of FY with FP and PP (positive). The genetic and phenotypic correlations between FP and PP were similar and moderate to high in both milking populations. However, the estimates of LP with FP and PP were closer to zero in both milking populations.

Correlations Between Production and Fertility Traits

In both milking populations, all the phenotypic correlations between milk production and fertility traits were weak and close to zero (OAD: -0.08 to 0.06 ; TAD: -0.09 to 0.08). Most of the genetic correlations between milk production and fertility traits were weak to moderately negative. The genetic and phenotypic correlations of SMFS and calving to first service (CFS) with other production and fertility traits were similar across milking systems.

The genetic correlations between yield and interval fertility traits were low and positive in TAD (from $+0.11$ to $+0.29$). Genetic correlations of all yield traits (MY, FY, PY, and LY) with SMFS and CFS were positive and relatively greater in cows milked OAD than in cows milked TAD. However, genetic correlations between MY, LY, and SMCO were lower (approximately zero) in cows milked OAD compared with TAD. Estimated genetic correlations of MY, PY, LY with FSCO were negative for cows milked OAD, but these genetic correlations were positive in the TAD milking population. In both milking populations, genetic correlations between all yields and binary fertility traits were negative, except for NIC. The estimated genetic correlations of yield traits with SR21, SR42, and CR21 tended to be greater in cows milked OAD compared with cows milked TAD. However, genetic correlation estimates between yields and PR42, PRFS, NIC, and

CR42 tended to be lower in cows milked OAD than those milked TAD. Genetic correlations between MY, LY, and PR42 in OAD cows were close to zero.

The genetic correlations of milk composition (FP, PP, and LP) and all interval fertility traits were very low (OAD: -0.16 to 0.23 ; TAD: -0.06 to -0.31) in both milking populations. In cows milked TAD, the genetic correlations between milk composition and all interval fertility traits were negative, but the genetic correlations of milk composition and binary fertility traits were positive. Compared with TAD milking cows, genetic correlations between FP, PP, LP, and binary fertility traits tended to be lower in OAD milking cows. Protein percentage was positively genetically correlated with SR21, SR42, PR21, PR42, PRFS, CR21, and CR42 in the TAD milking population (from $+0.16$ to $+0.30$). However, genetic correlations between PP and all binary fertility traits were lower (from -0.16 to $+0.26$) in the OAD milking population. The genetic correlations between LP and NIC or CR21 were negative and comparatively higher in OAD than TAD.

Correlations Among the Fertility Traits

The phenotypic correlations among fertility traits were similar in both OAD and TAD milking populations. In both milking populations, phenotypic correlations between SMCO and FSCO were strongly positive. The SMCO and FSCO were strongly positively phenotypically correlated with CIN. Phenotypic correlations of SMFS and CFS with SR21 were strongly negative in both milking systems. Likewise, phenotypic correlations of SMCO, FSCO, and CIN with PR21, PR42, CR21, and CR42 were strongly negative in both milking populations. Strong positive phenotypic correlations of similar magnitudes were observed for PR21, PR42 with CR21 and CR42 in TAD and PR42 with CR21 and CR42 in OAD.

All fertility traits were strongly genetically correlated in cows milked TAD, but the magnitudes of the genetic correlations varied from weak to strong in cows milked OAD. In the OAD milking cow population, genetic correlations between SMCO, FSCO, CIN, PR21, PR42, and other binary fertility traits were strong. However, genetic correlations between fertility traits of time to first service (SMFS and CFS) and submission (SR21 and SR42) with other binary fertility traits were weak to moderate. The genetic correlations among the binary fertility traits were strong, but they were stronger in the TAD milking population. The genetic correlations between all interval traits and all binary traits were strong and negative, and these were stronger in the TAD milking cow population.

DISCUSSION

Reproductive Performance

This study has found that first parity cows milked TAD produced greater yields of milk, fat, protein, and lactose than cows milked OAD. Fat and protein percentages were higher in OAD milking cows than TAD milking cows. These findings agree with the study by Lembeye et al. (2016), who also studied New Zealand dairy cows with a similar breed mix as the current study. The fertility outcomes of CIN, SR21, PRFS, and PR42 reported for TAD milking cows in current study are similar to the reported national averages for New Zealand dairy cows in the calving season from 2015 to 2016 to 2017–2018 (LIC and DairyNZ, 2021). The reproductive performance of cows milked OAD exceeded the reported national averages and is consistent with previous research that found that New Zealand cows milked in OAD herds had improved reproductive performance compared with those that were milked TAD (Hemming et al., 2018, Jayawardana et al., 2022). The better reproductive performance associated with OAD milking cows is hypothesized to be due to the reduced extent of negative energy balance in early lactation in cows milked OAD (Phyn et al., 2014).

Variance Components and Heritability

The heritability estimates for MY, FY, PY, FP, and PP in cows milked OAD obtained in this study are consistent with previously reported estimates by Lembeye et al. (2016), whose study population was multiparous OAD milking cows in New Zealand. Heritability estimates found in this study for MY, FY, and PY in cows milked TAD agree with other estimates in New Zealand dairy cattle (Sneddon et al., 2015; Lopez-Villalobos et al., 2020). The heritabilities for FP and PP in cows milked TAD are similar to those reported by Lembeye et al. (2016) in TAD milking cows. Heritability estimates for LP concur with previous findings by Lopez-Villalobos et al. (2020). The heritability estimates for yields (MY, FY, PY, and LY) were greater in the OAD milking population compared with the estimates obtained in the TAD milking population. These findings, suggest that higher genetic responses for these traits could be obtained in the OAD milking population, when the response is measured in genetic standard deviations. However, when expressed in absolute values the genetic responses would be expected to be greater in the TAD milking population than the OAD population because the genetic variances are greater in the TAD milking population.

The heritability estimates for SMFS, SMCO, FSCO, CFS, CIN, SR21, PR21, PR42, and CR42 ranged between 0.02 and 0.07 in cows milked TAD, in agreement with previously reported estimates in New Zealand (Grosshans et al., 1997; Harris et al., 2005; Pryce and Harris, 2006). Also, estimated heritabilities for fertility traits in this study are consistent with studies in Irish and Australian dairy cattle populations (Berry et al., 2013; Morton et al., 2018). In both milking systems, heritability estimates for fertility traits were lower than heritability estimates for production traits. This suggests that the phenotypic expression fertility traits are more influenced by management and environmental factors than genetic factors. The estimated covariance components and heritabilities in this study can be used for future genetic evaluation studies and to develop separated selection indices for OAD and TAD dairy cattle populations in New Zealand.

Correlations Between Production Traits

Overall, phenotypic and genetic correlations between production traits presented in Tables 4 and 5 are in line with previously reported estimates for New Zealand dairy cows milked in TAD and OAD populations (Ahlborn and Dempfle, 1992; Sneddon et al., 2015; Lembeye et al., 2016). The genetic correlations between FY and MY or PY in cows milked TAD in the current study are consistent with the findings of Lembeye et al. (2016). Greater genetic correlations were reported by Ahlborn and Dempfle (1992) and Sneddon et al. (2015) than our results (FY and MY: 0.55–0.82, FY and PY: 0.69–0.88, and FY and LY: 0.40). In agreement with the estimates reported by Costa et al. (2019), weak phenotypic and genetic correlations were observed between LP and FP or PP in this study (LP and FP: -0.02 and 0.01 , LP and PP: -0.02 and -0.01 , respectively). In both milking populations, most of the phenotypic and genetic correlations between milk yields and milk composition traits are similar in direction and magnitude.

Correlations Between Production and Fertility Traits

Estimates of genetic correlations between milk production and fertility traits obtained in this study were, in general, antagonistic in both milking populations. These estimates suggest that increases of production yields (MY, FY, PY) will result in longer intervals of SMFS, SMCO, FSCO, CFS, CIN, and decreases in SR21, SR42, PR21, PR42, PRFS, CR21, and CR42 in the TAD milking cow population. These unfavorable genetic correlations agree with most previous literature in New Zealand (Grosshans et al., 1997; Harris et al.,

2005; Pryce and Harris, 2006), Ireland (Evans et al., 2002; Berry et al., 2003), Australia (Haile-Mariam et al., 2003; Morton et al., 2018), and the United Kingdom (Pryce et al., 1998). Although cows milked OAD had better phenotypic reproductive performance (Jayawardana et al., 2022), we found that phenotypic associations between milk production and fertility traits were negligible. Further research is required to identify the causal factors that reduce phenotypic associations between milk production and fertility in both milking cow populations. The low phenotypic correlations between production and fertility traits suggest that there still is the potential to reduce the negative effect of high milk production on reproductive performance through improving management practices in both milking cow populations.

The negative genetic correlations between yields and FSCO are interesting in the OAD milking population, suggesting that increasing genetic merit for milk production decreases the length of FSCO in cows milked OAD. The genetic correlations of MY and LY with SMCO, PRFS, and PR42 were lower in cows milked OAD compared with cows milked TAD. These findings suggested that OAD milking cows with higher genetic merit for production had a shorter interval from SMCO, that is they are more likely to conceive to their first service and to get in-calf early in the breeding season than TAD milking cows. Furthermore, our results demonstrate the genetic correlation of MY and NIC is very low in cows milked OAD, and phenotypic correlations of NIC with milk composition (FP, PP, and LP) and production traits (MY, FY, PY, and LY) were also close to zero. This indicates the levels of production and milk composition are not associated with overall pregnancy rate in OAD milking populations. Edwards (2018) reported that fewer OAD milking cows were removed from the herd in New Zealand due to not being pregnant and more were removed due to the low production, udder health, and mastitis. However, our results indicate the genetic correlations for yields and SMFS, SR21, and CR21 are more unfavorable in the OAD compared with TAD. Reasons for this unfavorable association have not been identified in this study. This is an area where further research is required.

At present, 2 binary traits of SR21, CR42, and calving season day are used for genetic evaluation of fertility in New Zealand dairy cows (Bowley et al., 2015). The genetic correlations observed for MY, FY, PY with SR21 in TAD milking cows agree with the estimates reported by Pryce and Harris (2006) for first parity cows in New Zealand (-0.23 , -0.10 , and -0.13 , respectively). However, our estimates for the genetic correlations between MY, FY, PY, and CR42 in cows milked TAD are slightly greater than the estimates by Pryce and

Harris (2006; -0.15 , -0.06 , and -0.05 , respectively) and Harris et al. (2005; MY and CR42: -0.16) for first parity cows. To our knowledge, this is the first study that estimates the genetic and phenotypic correlations between MY and NIC in the New Zealand dairy cattle population. A positive genetic association was found with MY and NIC in cows milked TAD, suggesting that high-producing cows milked in TAD are more likely to be not in-calf. Morton et al. (2018) reported a positive genetic correlation between 120-d MY and NIC (0.23) in the Australian dairy cattle population, similar to our findings in TAD milking cows.

Results from the current study identified positive genetic associations of milk composition (FP, PP, and LP) with binary traits (except NIC) and negative associations with interval fertility traits in cows milked TAD. Those cows producing milk with higher percentages of fat, protein, and lactose are more likely to have better fertility in TAD milking cow population. In agreement with our findings, Morton et al. (2018) reported positive genetic associations between 120-d PP and SR21, PR42, and PRFS (0.28 , 0.28 , and 0.23 , respectively) and negative genetic associations for 120-d PP and CFS, CIN, and NIC (-0.32 , -0.23 , -0.17 , respectively). The genetic correlations identified between LP, PP, and CIN agree with those reported by Haile-Mariam and Pryce (2017; LP and CIN: -0.23 and PP and CIN: -0.28). Furthermore, Carty et al. (2020) reported LP measured at 0–30 DIM had the strongest relationship with SMCO in the Irish cattle population. The positive genetic associations observed for PP with SR21, PR21, PR42, PRFS, CR21, and CR42 in cows milked TAD suggest that genetic selection for increased PP would be expected to increase genetic merit for fertility in cows. Morton et al. (2017) suggested that the possible causes of the positive genetic association between reproductive traits and PP is due to selection for both high fertility and milk protein production.

The estimated genetic associations between PP and fertility traits in cows milked OAD differ from those in cows milked TAD. Many studies demonstrate that both milk composition and reproductive performance are influenced by early lactation energy balance of dairy cows (Friggens et al., 2007; Patton et al., 2007; van Knegsel et al., 2014). Benedet et al. (2020) reported early lactation blood BHB and nonesterified fatty acids were negatively genetically associated with PP and LP in Italian Holstein cows. Morton et al. (2016) reported that associations between PP and reproductive performance are probably partly due to factors other than extent of negative energy balance in early lactation. Therefore, further research should be carried out to estimate correlations between variables which are contributing to negative energy balance and PP in the

OAD milking population. Our results indicate LP is negatively genetically correlated with NIC and CR42 in the OAD milking population. Cows with low genetic merit for LP are more likely to be NIC and less likely to have calved by 3 wk in the following season in the OAD milking population.

Correlations Between Fertility Traits

The estimated genetic and phenotypic correlations between fertility traits in the TAD milking cow population agree with estimates reported by Grosshans et al. (1997). Correlations between SR21 and CR42 agree with findings by Harris et al. (2005) and Pryce and Harris (2006). Morton et al. (2018) reported genetic and phenotypic associations of PR42 with CFS, CIN, SR21, PRFS, and NIC for Australian dairy cows, values which are similar to those found in the TAD population in the current study.

Most of the phenotypic associations among fertility traits were consistent across the milking regimens. The reproductive management of OAD and TAD cows is similar, with most herds in New Zealand inseminating cows only once per day, most often in the morning. Mating periods on average are shorter in OAD herds (71.8 vs. 76.1 d; Hemming et al., 2018). The genetic and phenotypic associations among interval fertility traits were strongly positively correlated due in part to the whole relationships between them. We found most of the genetic correlations among SMFS, CFS, SR21, and SR42 and other fertility traits were low to moderate in cows milked OAD, whereas SMCO, FSCO, CIN, PR21, PR42, and other binary fertility traits are strongly genetically correlated in cows milked OAD. These findings suggest that in OAD milking herds, a cow's genetic merit for the ability to conceive has greater effect on her phenotypic expression of fertility than the ability to show estrus. The genetic correlations between fertility traits were stronger with low standard errors but not unity in cows milked TAD, and genetic correlations of fertility traits were weak to strong with higher standard errors in cows milked OAD; therefore, in OAD herds, emphasis on several fertility traits will be necessary to achieve progress, as correlated gains from emphasis on a single trait will be smaller than in TAD cows.

We found nonconverged and unrealistic genetic correlation estimates of CR42 with CIN, PRFS, NIC, and CR21 in the OAD milking cow population. Cows milked OAD had a higher 6-wk calving rate than TAD (89 vs. 82%). The binary trait CR42 included few zero values, and this may be a reason for the nonconverged algorithms in ASReml parameter estimation. Standard errors for genetic correlation estimates were relatively greater in cows milked OAD than cows milked TAD

due to relatively less amounts of data in the OAD milking population. Amer et al. (2016) reported when including more traits in a multitrait model, genetic parameters have remained stable but standard error increased substantially. Furthermore, Craig et al. (2018) reported that low heritabilities of the fertility traits and potential culling bias reflected high standard errors of the genetic correlation estimates, particularly for traits expressed in later parities.

Once-daily milking is becoming a popular milking practice in New Zealand, and about 31% of dairy farmers in the Northland region adopted full season OAD milking (DairyNZ, 2022). In this context, investigation of phenotypic and genetic relationships is important for OAD milking population. The growing use of early-aged pregnancy testing allowed us to derive PR21, PR42, and NIC using early-aged PD records, which is an accurate method of determining the conception date. In present analysis, cows that had missing AB records and conceptions were retained with penalized dates at the extreme end of the distribution in both milking cow populations. Previous studies in different dairy cattle populations also estimate the genetic correlations by assigning the penalty values for the cows that do not experience the event (Grosshans et al., 1997; Haile-Mariam et al., 2003; Morton et al., 2018). This approach introduces some bias, where some cows have an assigned value greater and some less than they would have achieved had they been allowed longer to display the trait. Nevertheless, to exclude these cows would have introduced a greater bias, in that the performance of the least fertile cows was not considered.

Because this is the first study to estimate genetic and phenotypic correlations for fertility traits for the OAD milking cow population, we do not have other estimates to compare with our findings. The current system of genetic evaluation for fertility traits does not separate the cows or sires according to milking regimens in New Zealand. The estimated genetic and phenotypic correlations in cows milked OAD can be used to develop fertility breeding values specifically for the OAD milking cow population and to develop separate selection indices for the OAD and TAD dairy cattle populations. Further research is required to evaluate the interaction between genotype by milking frequency for fertility traits in New Zealand and other countries adopting OAD milking systems.

CONCLUSIONS

In this study we found heritability estimates for milk composition and fertility traits were similar for cows that were milked either OAD or TAD in seasonal calving New Zealand dairy herds. The genetic and pheno-

typic associations between milk production traits were similar regardless of the milking regimen. Phenotypic correlations between milk production and fertility traits were negligible. However, genetic correlations between milk production and fertility were antagonistic in both milking populations. The genetic correlations between milk production and the key reproductive metrics of PR42, NIC, and CR42 were smaller in cows milked OAD than TAD. This implies that the difference in the milking regimen or other management practices in OAD milking herds could have lessened the antagonistic genetic association between those traits. Milk protein concentration was positively genetically correlated with fertility traits in the TAD milking cow population. This indicates that there is the potential to increase the fertility performance of dairy cattle by identifying the mechanisms of the association between PP and fertility traits in cows milked TAD. Further studies are required to identify these associations for cows milked OAD. The present findings can be used to develop separate selection indexes for OAD milking population.

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