



## Estimation of genetic parameters and individual and maternal breed, heterosis, and recombination loss effects for production and fertility traits of spring-calved cows milked once daily or twice daily in New Zealand

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### ABSTRACT

The objectives of this study were to estimate genetic parameters and individual and maternal breed, heterosis, and recombination loss effects for milk production and fertility traits of Holstein Friesian (F), Jersey (J), and crossbred Holstein Friesian and Jersey (F × J) cows milked once daily (OAD) or twice daily (TAD) in New Zealand. Data on 278,776 lactations from 30,217 OAD and 170,680 TAD milking cows across 644 spring-calving herds were available. Genetic parameters and individual and maternal breed, heterosis, and recombination loss estimates were obtained from univariate animal models. Heritability and repeatability estimates for milk production, milk composition, and fertility traits were consistent across the milking frequencies. Heritability estimates for yields of milk, fat, protein, and lactose varied between 0.21 and 0.29 in OAD and TAD. Heritability estimates for fertility traits ranged from 0.01 to 0.08 in both populations, and estimates were slightly greater in TAD than OAD milking cows. In both milking populations, individual breed effects for yields were in favor of F cows; however, maternal breed effects for yields were in favor of J dams. Jersey cows were more fertile than the F cows in both milking populations, but maternal breed effects for fertility traits were in favor of F dams. Individual heterosis effects were favorable for all traits and were consistent across milking regimens. Crossbred F × J cows had significantly shorter intervals from start of mating to first service and from start of mating to conception, and a higher proportion of 3-wk submission, 3-wk in calf, and 3-wk calving relative to the average of purebred F and J cows. Recombination loss effects were not always unfavorable for production and fertility traits, but most estimates were small with larger standard

errors. Favorable maternal heterosis effects were associated with production traits in both milking systems, but maternal heterosis effects were less likely to influence reproductive performance.

**Key words:** once daily milking, fertility, crossbreeding, heritability

### INTRODUCTION

Estimates of genetic parameters for milk production and fertility traits have been reported in seasonal dairy-producing systems (Grosshans et al., 1997; Pryce et al., 1998; Berry et al., 2013); however, most reported genetic parameters for production and fertility traits are associated with data from cows milked twice daily (TAD). Since the late 1990s, some farmers in New Zealand have been milking their cows once daily (OAD) for the entire lactation (Davis et al., 1999), and about 9% of herds that underwent herd-testing in the production season 2015–2016 were milked OAD for the whole lactation (Edwards, 2018). Some studies have reported that cows milked OAD for the entire lactation have better reproductive performance than cows milked TAD for the entire lactation (Clark et al., 2006; Edwards, 2018; Hemming et al., 2018). Estimates of genetic parameters for fertility traits in the OAD milking cow population have not been reported.

Since 1985, crossbreeding has been adopted as the predominant mating strategy in New Zealand (Montgomerie, 2005). At present, the breed composition of the national herd comprises crossbred Holstein Friesian × Jersey cows (F × J; 49.6%), Holstein Friesian (F; 32.5%), Jersey (J; 8.2%), other breeds and crosses (9.3%), and a small proportion of Ayrshire (0.4%; LIC and DairyNZ, 2021). In New Zealand, a cow's lifetime ability to convert feed into farm profit is measured using the Production Worth (PW) Index (Harris, 2005). The PW Index is calculated as the sum of estimated production values for lactation yields of milk, fat and protein, cow mature live weight, and SCS, each multi-

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plied by the corresponding economic value. The production values are calculated as the sum of estimated breeding value, permanent environment effect, and heterosis effect (Harris et al., 2007).

The breed and heterosis effects for milk production traits have been reported in grazing dairy cattle milked TAD and OAD in New Zealand (Harris and Kolver, 2001; Lembeye et al., 2015); however, the breed, heterosis, and recombination loss effects for fertility traits have not been investigated among cows milked OAD. Earlier, Ahlborn-Breier and Hohenboken (1991) estimated individual and maternal breed and heterosis effects for yields of milk and fat, as well as fat percentage for New Zealand dairy cows milked TAD; however, maternal heterosis effects for protein and lactose yield, milk composition, and fertility traits have not been estimated. If heterosis effects for the OAD milking population are different from those of the TAD milking population, bias could be introduced into the calculation of production values. Therefore, it is important to calculate heterosis effects for the OAD milking population.

The present study had 2 objectives: first, to estimate genetic parameters (variance components, heritability, and repeatability) for production and fertility traits in the OAD milking population; second, to estimate the individual and maternal breed, heterosis, and recombination loss effects for production and fertility traits of OAD and TAD milking cows.

## MATERIALS AND METHODS

### Herd Selection

Because no live animals were used in this study, institutional animal care and use committee approval was not required. Animal records on herd-test milk yields, calving, mating, pregnancy diagnosis, lactation yields, and ancestry information of dairy cows in 3 spring-calving seasons from 2015–2016 to 2017–2018 in New Zealand were extracted from the Livestock Improvement Corporation database. The key criteria in herd selection for the present study were as follows: at least 50 cows in the herd, at least 4 herd tests in a given lactation, pregnancy test results recorded for at least 80% of cows that calved in the 12-mo period, and “early aged pregnancy testing” (tested on or between 35 and 122 d of pregnancy) and fetal age estimated for at least 80% of cows in the herd. A total of 2,421 spring-calving herds with 1,632,461 cows and 2,704,600 lactations met these criteria.

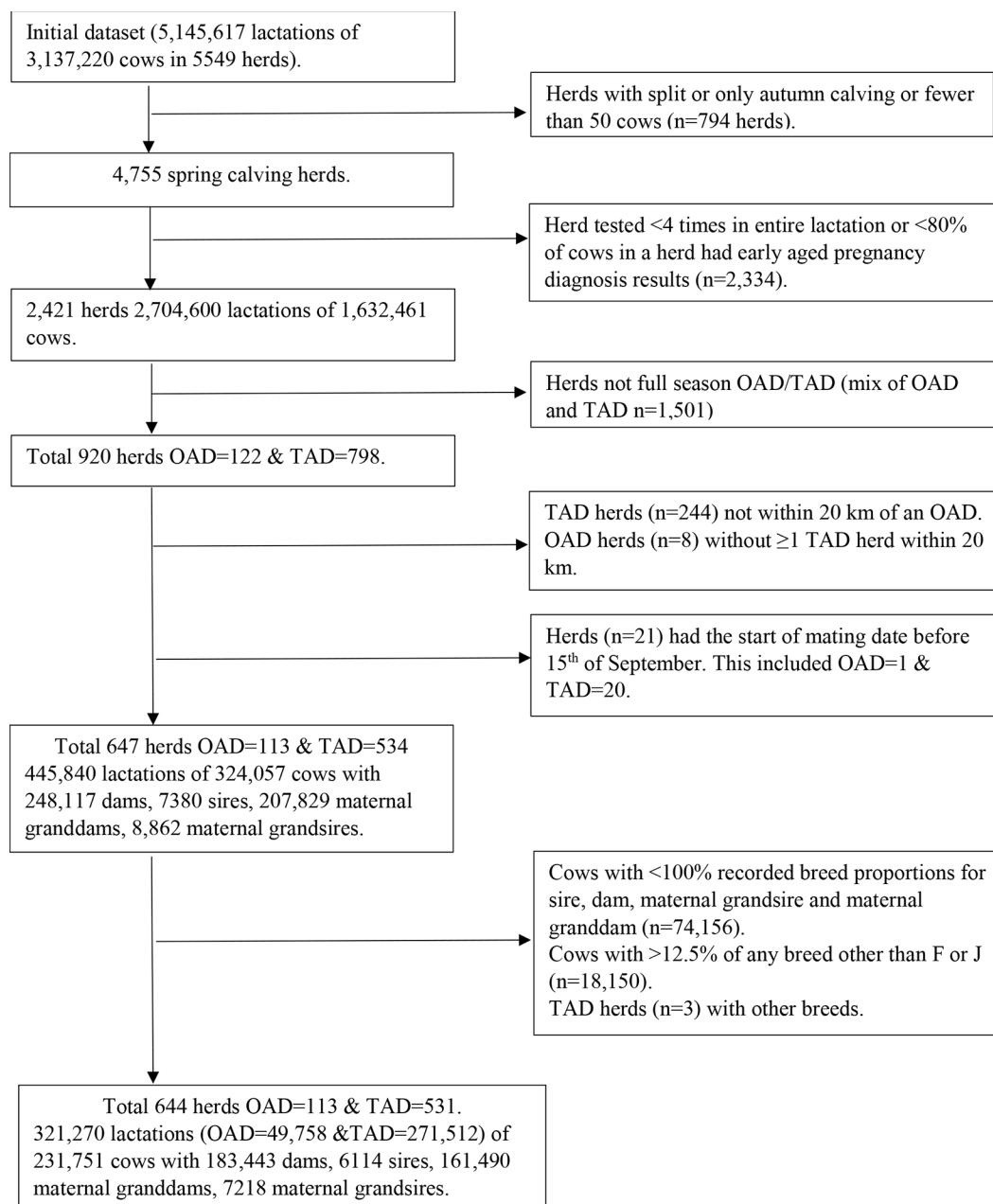
Herds were classified into 2 categories, OAD or TAD milking throughout the entire lactation, using

the information on herd-test day milking frequency. If more than 90% of the tested cows on a herd-test date were milked either OAD or TAD in a herd, then it was classified as OAD or TAD milking herd on that herd-test date. All herd tests were classified from the 2015–2016 to 2017–2018 seasons. If all the herd tests were classified as OAD throughout the period, then the herd was identified as an OAD milking herd, whereas if all herd tests were classified as TAD, then the herd was identified as a TAD herd. Herds with both OAD and TAD tests were excluded from the analysis. The geographical proximity of herds was determined using GPS Visualizer (Schneider, 2012), and any herds that were more than 20 km from the nearest herd of opposite milking frequency were excluded from the analysis. A total of 668 herds were identified, made up of 114 OAD and 554 TAD herds. Herds where the start of the breeding season occurred before September 15 in each spring calving season were removed ( $n = 21$ ) from the data set. Cows and their sire, dam, maternal granddam, and maternal grandsire with more than 12.5% of a breed other than F or J were excluded ( $n = 18,150$ ). Consequently, herds without F, J, and crossbred F  $\times$  J cows were excluded (3 TAD herds). Finally, 113 OAD and 531 TAD herds with 231,751 cows were selected in this study (Figure 1).

### Production Data Set

Lactation records of milk (MY), fat (FY), protein (PY), and lactose (LY) yields (kg) with DIM ranging from 150 to 305 were included (243,250). Lactations with milk yield 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 removed ( $n = 4,302$ ) due to uncertainty of the records. The means of MY, FY, PY, and LY were 4,657, 224, 180, and 234 kg, respectively (Table 1). Fat percentage (FP), protein percentage (PP), and lactose percentage (LP) were calculated for each lactation record as the ratio between FY, PY, or LY and MY multiplied by 100.

Age at calving was calculated for cows in each parity. Cows in first lactation that were greater than 900 d of age at calving were excluded ( $n = 1,263$ ; 1.7%). Age at second, third, and fourth calving was restricted to be between 1,000 and 1,200 d, 1,350 and 1,600 d, and 1,750 to 2,000 d, respectively. Age restriction for fifth and greater than fifth calvings is detailed in Figure 2. Lactation records were grouped into 5 parity classes, cows with parity numbers 5 to 10 were grouped into parity 5, and cows with more than 10 parities were excluded ( $n = 1,458$ ).



**Figure 1.** Flowchart detailing inclusion of herds that cows milked once daily (OAD) or twice daily (TAD) during the entire lactation. F = Holstein Friesian; J = Jersey.

### Reproduction Data Set

Calving dates between June 1 and December 31 in each calving season were retained ( $n = 306,126$ ). Mating start and end dates were sourced 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 1 mating recorded, where at least 3 of the next 6 d also have mating records

(DairyNZ, 2019). The mating end date of the herd was defined as follows: (1) the last recorded mating date on or before the 21st week of the mating period, (2) the last date with 2 conceptions followed by at least 30 d with no conceptions on or before the 21st week of the mating period, or (3) the last date with 1 conception on or before the 21st week of the mating period that was followed by at least 30 d with no conceptions and had at least 1 conception on each of 2 or more other days

**Table 1.** Trait abbreviations, descriptions, means, and SD of traits in selected cow population

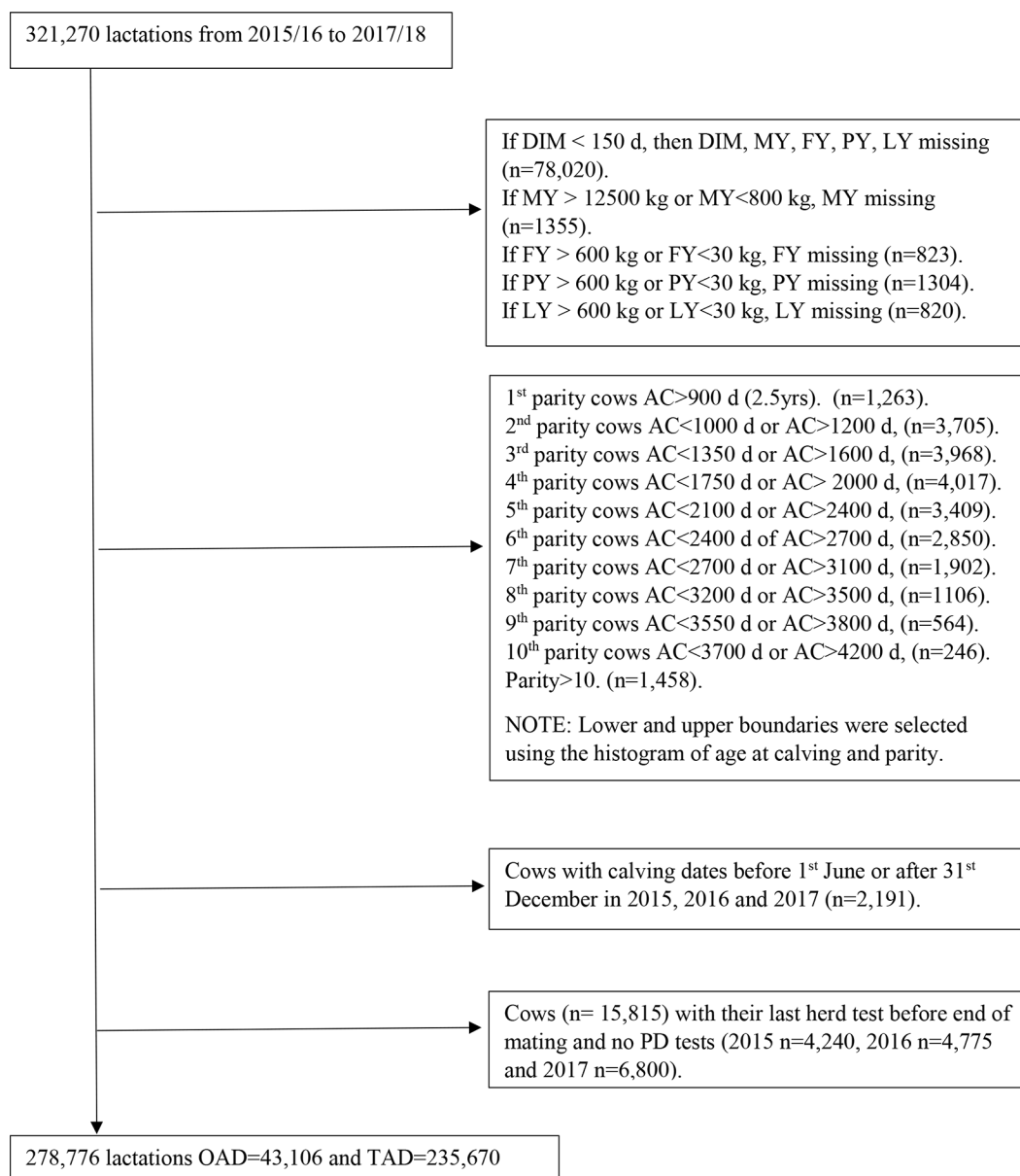
Abbreviation	Description	Mean	SD
<b>Production trait</b>			
MY	305-d milk production (kg)	4,657	1,441
FY	305-d fat production (kg)	224	64
PY	305-d protein production (kg)	180	52
LY	305-d lactose production (kg)	234	73
FP	Fat percentage, kg fat per kg milk (%)	4.9	0.8
PP	Protein percentage, kg protein per kg milk (%)	3.9	0.3
LP	Lactose percentage, kg lactose per kg milk (%)	5.0	0.2
<b>Fertility trait</b>			
SMFS	Interval from the start of mating to the first service (d)	12.1	10.2
SMCO	Interval from the start of mating to conception (d)	24.3	19.8
FSCO	Interval from the first service to conception (d)	11.9	17.9
CFS	Interval from calving to the first service (d)	77.3	19.8
CInt	Interval between 2 consecutive calvings (d)	369.3	24.5
SR21	Presentation (1) or non-presentation (0) for mating within the first 21 d of the start of the mating (binary)	0.82	0.4
SR42	Presentation (1) or non-presentation (0) for mating within the first 42 d of the start of the mating (binary)	0.94	0.2
PR21	Conceived (1) or not conceived (0) within the first 21 d of mating (binary)	0.47	0.5
PR42	Conceived (1) or not conceived (0) within the first 42 d of mating (binary)	0.69	0.5
PRFS	Conceived (1) or not conceived (0) to first service (binary)	0.56	0.5
NIC	Not in calf (1) or in calf (0) by end of the mating period (binary)	0.13	0.3
CR21	Calved within the first 21 d of the planned start of calving date of herd in the subsequent season (1) or calved after the first 21 d from the planned start of calving date of herd in the subsequent season (0). Cows that did not calve in the subsequent season were treated as missing variables (binary).	0.58	0.5
CR42	Calved within the first 42 d of the planned start of calving date of herd in the subsequent season (1) or calved after the first 42 d from the planned start of calving date of herd in the subsequent season (0). Cows that did not calve in the subsequent season were treated as missing variables (binary).	0.83	0.4

in the 6 preceding days (DairyNZ, 2019). The average length of the breeding season was 76.1 d across herds in the study. If any recorded mating dates were outside the herd's mating period, then those mating records were not used for the fertility trait calculations ( $n = 1,034$ ). Cows with an interval from calving to first service (**CFS**) less than 7 d were excluded ( $n = 20$ ). Pregnancy diagnosis testing was conducted using transrectal ultrasound or rectal palpation. Cows that were missing both a pregnancy diagnosis record 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 excluded from the data set ( $n = 15,815$ ).

Following editing of the data as described, 43,106 OAD and 235,670 TAD lactations across 644 herds were included in the analysis (Figure 2). The data set included 200,897 cows with pedigree over 5 generations of 160,992 dams, 5,485 sires, 142,383 maternal granddams, and 6,588 maternal grandsires. The distribution of cow by breed was 72,279 (36.0%) F, 20,803 (10.4%) J, and 107,815 (53.7%) F  $\times$  J cows, and distribution of cows by dam breed was 74,792 (37.2%) F dam, 24,600 (12.3%) J dam, and 101,505 (50.5%) F  $\times$  J dams. The distribution of cows by breed and parity in the OAD and TAD milking is presented in Table 2.

### Fertility Traits

A range of fertility traits was defined to reflect the features of seasonal calving and breeding in New Zealand dairy cows (Table 1). The estimation of the genetic parameters will be biased if cows with no artificial breeding (**AB**) or no conceptions are excluded for time-to-event variable analysis. Therefore, cows with no recorded AB inseminations ( $n = 12,602$ ) were retained for the genetic parameter estimation of intervals from start of mating to the first service (**SMFS**) and CFS, and they were assigned the first service date as the end of the AB period in each herd within the calving season. The end of the AB period was defined for each herd as the date of the last AB insemination that was not followed by another AB inseminations within 7 d. Cows that had not conceived ( $n = 42,613$ ) at the end of the mating season were also retained, and they received penalty dates for conception. The conception dates were assigned for nonpregnant cows as the mating end date in each herd plus 21 d (Johnston and Bunter, 1996; Grosshans et al., 1997). Consequently, intervals from the start of mating to conception (**SMCO**) and the first service to conception (**FSCO**) included the information of nonpregnant cows with the projected



**Figure 2.** Flowchart detailing inclusion of cows in production and reproduction data sets. OAD = once-daily milking; TAD = twice-daily milking; AC = age at calving; MY = milk yield; FY = fat yield; PY = protein yield; LY = lactose yield; PD = pregnancy diagnosis.

penalized conception dates. Further, cows that did not calve the following season, despite a positive pregnancy diagnosis (84,095) were retained for estimation of the genetic parameters for calving interval (**CInt**). These cows were assigned a calving date 282 d from the conception dates, and **CInt** was calculated as the assigned calving dates minus the calving date in the respective season.

Submission by 3 wk (**SR21**) or 6 wk (**SR42**) of the breeding season was coded as 1 if the first mating date was in the first 21 d or 42 d from the start of mating

date, respectively, otherwise coded as 0. The conception to the first service (**PRFS**) was only calculated for cows with a first service date and was coded as 1 if the first service date was equal to the conception date and otherwise 0 (Appendix Figure A1). Cows with recorded mating dates that were outside the mating period were recorded as missing for the calculation of **SR21**, **SR42**, and **PRFS** due to uncertainty of the records. Details for the calculation of conception dates, in calf by 3 wk (**PR21**), in calf by 6 wk (**PR42**), and not in calf (**NIC**) are presented in Figure 3. Conception dates

were calculated as the date of pregnancy diagnosis testing minus the estimated pregnancy day count for cows with a pregnancy status of “pregnant.” If cows with positive pregnancy diagnosis had estimated pregnancy day counts outside the bounds (<35 d or >122 d) or no estimated fetal age results, but calved in the subsequent season, their conception dates were calculated as subsequent calving dates minus gestation length of 282 d. Cows were defined as NIC if they were recorded as not pregnant at last pregnancy testing date after the end of the mating period. Planned start of calving date was derived for a herd by adding 282 d to the herd’s mating start date in each calving season. The calculations of calving by 3 wk (CR21) and 6 wk (CR42) from the planned start of calving in the subsequent calving season are presented in Figure 4.

The summary statistics for the fertility traits in the selected population are shown in Table 1. The proportions of cows mated within the first 3 wk and 6 wk of the breeding season were 82% and 94%, respectively. A total of 56% of the cows were pregnant to their first service, and 47% and 69% of cows conceived by the first 3 wk and 6 wk of the breeding season, respectively. Only 13% of cows in the data set were not in calf at the end of breeding seasons. Average calving rates by 3 wk and 6 wk were 58% and 83%, respectively. Reproductive performances by milking regimens in OAD and TAD were as follows: 86.5% and 80.8% for SR21, 77.6% and 67.7% for PR42, 62.6% and 54.5% for PRFS, 63.9% and 57.0% for CR21, 87.2% and 81.6% for CR42, and 9.4% and 13.9% for NIC, respectively.

### Individual and Maternal Heterosis and Recombination Loss Coefficients

The coefficients for individual and maternal heterosis and recombination loss were calculated using the animal ancestral information with 16th breed proportions. The individual and maternal heterosis coefficients ( $h_{F \times J}$ ) were calculated using the following equation (Dickerson, 1973):

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

When calculating the individual heterosis coefficient for progeny,  $\alpha_F^S$  and  $\alpha_J^S$  represent breed proportions of F and J in the sire (S), respectively; and  $\alpha_J^D$  and  $\alpha_F^D$  represent breed proportions of J and F in the dam (D), respectively. When calculating the maternal heterosis coefficients of dam,  $\alpha_F^S$  and  $\alpha_J^S$  represent breed proportions of F and J in the maternal grandsire, respectively; and  $\alpha_J^D$  and  $\alpha_F^D$  represent breed proportions of J and F in the maternal granddam, respectively.

**Table 2.** Distribution of cows by breed, parity, and production means (SD) according to milking regimen

Item	Once-daily milking	Twice-daily milking
<b>Breed</b>		
Holstein Friesian (F)	4,148	68,131
Jersey (J)	7,637	13,166
Crossbred (F × J)	18,432	89,383
<b>Parity</b>		
1	10,648	58,220
2	5,967	31,119
3	3,892	22,625
4	3,219	17,664
≥5	6,491	41,052
<b>Production</b>		
Milk yield (kg)	3,253 (919)	4,929 (1,363)
Fat yield (kg)	170 (45)	234 (62)
Protein yield (kg)	134 (36)	189 (50)
Lactose yield (kg)	161 (46)	248 (69)
Fat (%)	5.31 (2.1)	4.82 (0.7)
Protein (%)	4.15 (3.0)	3.86 (0.3)
Lactose (%)	4.97 (0.2)	5.04 (0.2)

Individual and maternal recombination loss coefficients ( $r$ ) were calculated using the following equation (VanRaden and Sanders, 2003):

$$r = 1 - \sum_{i=1}^2 \frac{sire_i^2 + dam_i^2}{2},$$

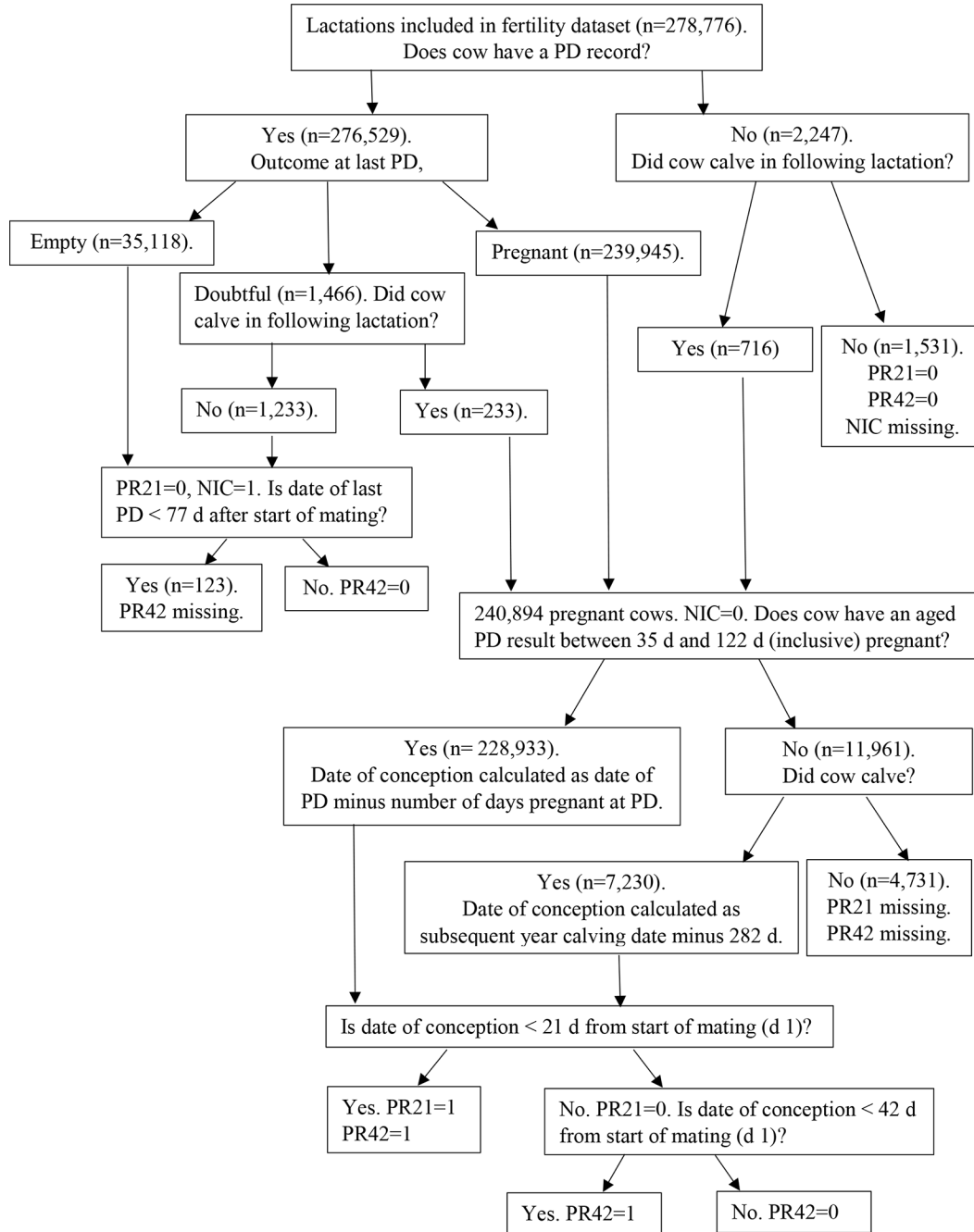
where  $sire_i$  and  $dam_i$  are the proportion of breed  $i$  in the sire and dam, respectively. In calculation of maternal recombination loss coefficients,  $sire_i$  and  $dam_i$  are the proportion of breed  $i$  in the maternal grandsire and maternal granddam.

### Statistical Analysis

Contemporary groups were defined as the group of cows calving in the same herd and year. Variance components, heritability, repeatability, individual and maternal breed, and heterosis effects were estimated using the ASReml 4.1 software package (Gilmour et al., 2015). Variance components for animal additive genetic variance ( $\sigma_a^2$ ), cow permanent environment variance ( $\sigma_c^2$ ), and random residual variance ( $\sigma_e^2$ ) for each production and fertility trait were obtained using the following single-trait repeatability animal model:

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

where  $\mathbf{y}$  is the vector of observations for each production and fertility trait;  $\mathbf{b}$  is the vector of fixed effects;  $\mathbf{a}$  is the vector of animal additive genetic effects;  $\mathbf{p}$  is the vector of random cow permanent environment effects;  $\mathbf{e}$  is the vector of random residual effects; and  $\mathbf{X}$ ,  $\mathbf{Z}$ ,



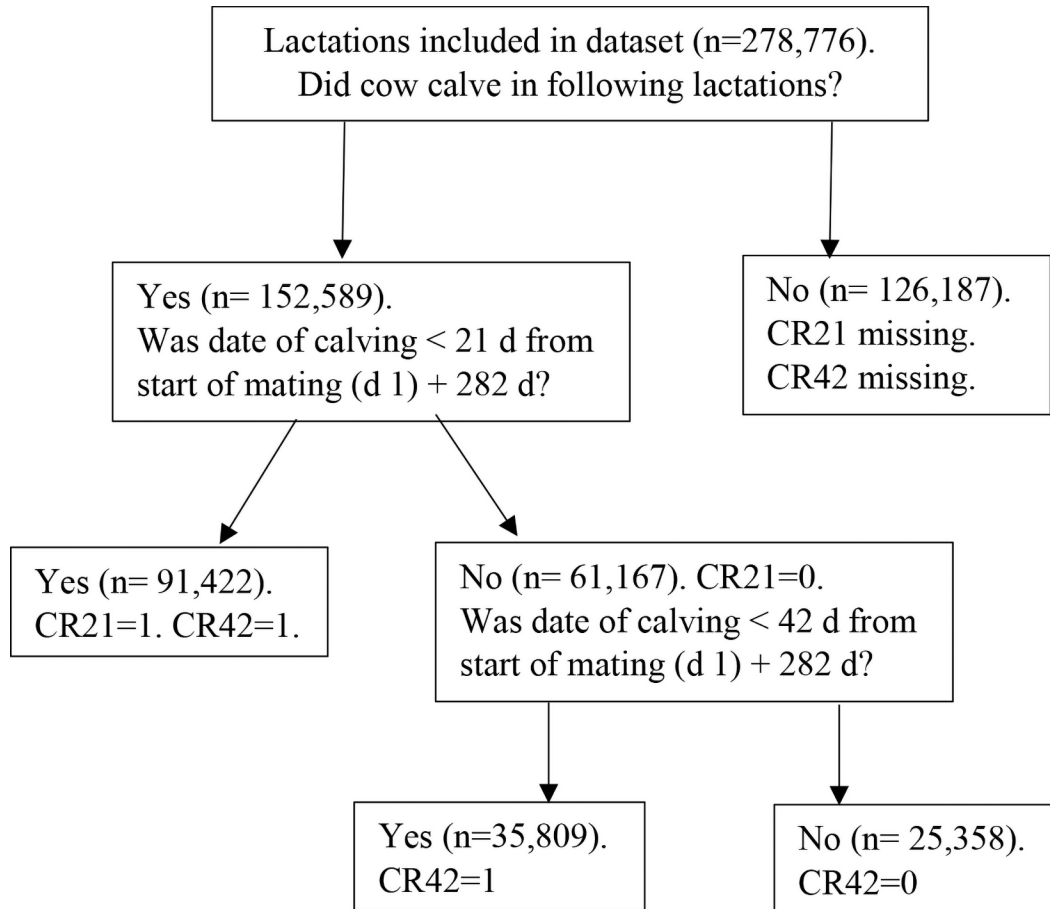
**Figure 3.** Flowchart detailing determination of 3-wk in calf (PR21), 6-wk in calf (PR42), and not in calf at end of the mating period (NIC) after pregnancy diagnosis (PD).

and **W** are incidence matrices relating the phenotypic records to the fixed, animal additive genetic, and cow permanent environment effects, respectively.

The fixed effects included in the model were contemporary group, parity (1, 2, 3, 4, and  $\geq 5$ ), the regression coefficients associated with the linear effect of the proportion of F in the cow and dam, the regression coefficients associated with individual and maternal

heterosis effects, the regression coefficients associated with individual and maternal recombination loss, and the regression coefficients associated with linear and quadratic effects of deviation of calving date from median calving date of the herd within season, respectively.

Variance components related to binary fertility responses in Table 1 (SR21, SR42, PR21, PR42, PRFS, NIC, CR21, and CR42) were analyzed in a logit scale



**Figure 4.** Flowchart detailing determination of 3-wk calving (CR21) and 6-wk calving (CR42).

with the random residual variance of  $\pi^2/3 = 3.2899$ . Final results were subjected to back-transformation to linear scale for interpretation of individual and maternal breed and heterosis effects.

The estimate of heritability ( $h^2$ ) for each trait was calculated as the proportion between the animal additive genetic and phenotypic variances, as follows (Falconer and Mackay, 1996):

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

Repeatability ( $t$ ) of each trait was calculated as

$$t = (\sigma_a^2 + \sigma_c^2) / \sigma_p^2,$$

where  $\sigma_a^2$  is the animal additive genetic variance,  $\sigma_c^2$  is cow permanent environment variance, and  $\sigma_p^2$  is the phenotypic variance for any trait, calculated as  $\sigma_p^2 = \sigma_a^2 + \sigma_c^2 + \sigma_e^2$ .

## RESULTS

### Variance Components, Heritability, and Repeatability

Estimates of variance components, heritability, repeatability, and their standard errors for production and fertility traits for cows in OAD and TAD populations are presented in Table 3 and Table 4, respectively. Animal genetic additive, permanent, and residual variances for MY, FY, PY, LY, and interval fertility traits (SMFS, SMCO, FSCO, CFS, CInt) were greater in the TAD milking population than in the OAD milking population.

In both populations, heritability estimates for MY, FY, PY, and LY were similar, and values ranged from 0.22 to 0.27 in OAD and from 0.21 to 0.29 in TAD. Milk compositional traits (FP, PP, and LP) had greater heritabilities than their respective yields. Although heritability estimates for FY and PY are equivalent to LY in both milking systems, FP and PP (0.58 and 0.68 in OAD vs. 0.66 for both in TAD) were more heritable than LP (0.36 and 0.35 in OAD and TAD, respectively).

**Table 3.** Estimates of variance components, heritabilities, and repeatabilities for milk production and fertility traits for once-daily milking (OAD) cow population

Trait	Variance component <sup>1</sup>				Heritability (SE)	Repeatability (SE)
	$\sigma_a^2$	$\sigma_c^2$	$\sigma_e^2$	$\sigma_{Total}^2$		
Production <sup>2</sup>						
MY	91,163	92,306	153,940	337,409	0.270 (0.015)	0.544 (0.007)
FY	223	239	507	969	0.231 (0.014)	0.477 (0.007)
PY	120	150	268	538	0.223 (0.014)	0.502 (0.007)
LY	244	248	404	896	0.273 (0.015)	0.549 (0.007)
FP	0.20	0.06	0.08	0.35	0.580 (0.016)	0.764 (0.004)
PP	0.04	0.01	0.01	0.06	0.684 (0.015)	0.835 (0.003)
LP	0.01	0.01	0.01	0.03	0.359 (0.016)	0.618 (0.006)
Fertility <sup>3</sup>						
SMFS	2.38	2.58	102.25	107.21	0.022 (0.005)	0.046 (0.007)
SMCO	11.86	9.18	686.57	707.68	0.017 (0.004)	0.030 (0.007)
FSCO	3.90	2.87	419.15	425.93	0.009 (0.003)	0.016 (0.006)
CFS	2.38	2.58	102.25	107.21	0.022 (0.005)	0.046 (0.007)
CInt	3.32	2.66	300.33	306.31	0.011 (0.003)	0.020 (0.006)
SR21	0.20	0.19	3.29	3.68	0.055 (0.011)	0.107 (0.011)
SR42	0.30	0.26	3.29	3.84	0.077 (0.021)	0.144 (0.019)
PR21	0.04	0.06	3.29	3.39	0.012 (0.004)	0.029 (0.006)
PR42	0.08	0.08	3.29	3.45	0.023 (0.006)	0.046 (0.008)
PRFS	0.03	0.06	3.29	3.38	0.007 (0.004) NS	0.026 (0.007)
NIC	0.13	0.09	3.29	3.50	0.036 (0.012)	0.061 (0.015)
CR21	0.06	0.04	3.29	3.40	0.019 (0.007)	0.032 (0.008)
CR42	0.07	0.07	3.29	3.43	0.021 (0.012) NS	0.042 (0.015)

<sup>1</sup> $\sigma_a^2$  = animal additive genetic variance;  $\sigma_c^2$  = cow permanent environmental variance;  $\sigma_e^2$  = random residual variance;  $\sigma_{Total}^2$  = total of phenotypic variance.

<sup>2</sup>MY = milk yield (kg); FY = fat yield (kg); PY = protein yield (kg); LY = lactose yield (kg); FP = fat percentage; PP = protein percentage; LP = lactose percentage.

<sup>3</sup>SMFS = 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); CInt = consecutive calving interval (d); SR21 = cows inseminated in the first 21 d from the start of mating; SR42 = cows inseminated in the first 42 d from the start of mating; PR21 = cows conceived in the first 21 d from the start of mating; PR42 = cows conceived in the first 42 d from the start of mating; PRFS = cows that conceived to their first service; NIC = cows not in calf at end of the breeding season; CR21 = cows that calved in the first 21 d from the planned start of the calving; CR42 = cows that calved in the first 42 d from the planned start of the calving. All heritability and repeatability estimates were significantly different from zero ( $P < 0.001$ ) except heritability estimates of PRFS and CR42 (NS indicates nonsignificant estimates).

Heritability estimates for fertility traits were low ( $\leq 0.08$ ) in both populations. Heritabilities for SMFS, SMCO, FSCO, CFS, and CInt were low and consistent between OAD (0.01 to 0.02) and TAD populations (0.02 to 0.04). Submission by 3 wk and 6 wk had the greatest heritabilities in both populations. The lowest heritability estimate was for PRFS in OAD (0.01), whereas both PRFS and CR21 had the lowest heritability in TAD (0.02). Heritability estimates for PR21 and PR42 were 0.01 and 0.02 in OAD, and 0.03 and 0.04 in TAD, respectively. Heritabilities for CR21 and CR42 were similar across milking frequencies (0.02).

Repeatability estimates for yield traits were similar across milking frequencies, with values ranging from 0.48 to 0.57. Like the heritability estimates, repeatability estimates for milk composition (FP, PP, and LP) were higher (ranging between 0.47 and 0.84) than their respective estimates for yields, and LP had the lowest repeatability compared with FP and PP in OAD and

TAD. However, repeatability for LP was higher in OAD than TAD (0.62 vs. 0.47). In both populations, repeatability estimates for fertility traits were low (ranging between 0.02 and 0.14) and similar across milking frequencies. The greatest repeatability was estimated for SR42 in OAD (0.14) and SMFS and CFS in TAD (0.11). The repeatability estimates for SMFS and CFS were similar within each population.

### Individual Breed, Heterosis, and Recombination Effects

Table 5 shows the estimates of individual and maternal breed and heterosis effects of cows milked in OAD and TAD milking populations. Breed effect is expressed as the difference in performance between F and J breeds.

For individual breed effects, F cows were superior for milk yields compared with J cows in both milking

**Table 4.** Estimates of variance components, heritabilities, and repeatabilities for milk production and fertility traits for twice-daily milking (TAD) cow population

Trait	Variance component <sup>1</sup>				Heritability (SE)	Repeatability (SE)
	$\sigma_a^2$	$\sigma_c^2$	$\sigma_e^2$	$\sigma_{Total}^2$		
Production <sup>2</sup>						
MY	198,272	193,621	301,506	693,399	0.286 (0.007)	0.565 (0.003)
FY	335	450	778	1,562	0.214 (0.007)	0.502 (0.003)
PY	174	253	420	848	0.206 (0.007)	0.504 (0.003)
LY	502	492	781	1,775	0.283 (0.007)	0.560 (0.003)
FP	0.23	0.06	0.06	0.35	0.656 (0.007)	0.814 (0.001)
PP	0.04	0.01	0.01	0.06	0.646 (0.006)	0.817 (0.001)
LP	0.01	0.003	0.02	0.03	0.352 (0.007)	0.471 (0.004)
Fertility <sup>3</sup>						
SMFS	3.54	12.56	127.28	143.38	0.025 (0.003)	0.112 (0.004)
SMCO	35.65	33.30	896.01	965.00	0.037 (0.003)	0.072 (0.005)
FSCO	13.16	18.21	563.42	594.80	0.022 (0.002)	0.053 (0.005)
CFS	3.55	12.54	127.27	143.35	0.025 (0.003)	0.112 (0.004)
CInt	8.47	0.19	380.98	389.63	0.022 (0.002)	0.022 (0.004)
SR21	0.26	0.02	3.29	3.56	0.073 (0.006)	0.077 (0.005)
SR42	0.29	0.006	3.29	3.58	0.080 (0.097)	0.081 (0.009)
PR21	0.10	1.44E-07	3.29	3.39	0.028 (0.002)	0.028 (0.002)
PR42	0.12	1.44E-07	3.29	3.41	0.035 (0.003)	0.035 (0.003)
PRFS	0.06	0.01	3.29	3.36	0.017 (0.002)	0.021 (0.003)
NIC	0.16	1.37E-07	3.29	3.45	0.046 (0.004)	0.049 (0.004)
CR21	0.05	1.42E-07	3.29	3.34	0.016 (0.002)	0.016 (0.002)
CR42	0.08	1.41E-07	3.29	3.37	0.025 (0.004)	0.025 (0.004)

<sup>1</sup> $\sigma_a^2$  = animal additive genetic variance;  $\sigma_c^2$  = cow permanent environmental variance;  $\sigma_e^2$  = random residual variance;  $\sigma_{Total}^2$  = total of phenotypic variance.

<sup>2</sup>MY = milk yield (kg); FY = fat yield (kg); PY = protein yield (kg); LY = lactose yield (kg); FP = fat percentage; PP = protein percentage; LP = lactose percentage.

<sup>3</sup>SMFS = 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); CInt = consecutive calving interval (d); SR21 = cows inseminated in the first 21 d from the start of mating; SR42 = cows inseminated in the first 42 d from the start of mating; PR21 = cows conceived in the first 21 d from the start of mating; PR42 = cows conceived in the first 42 d from the start of mating; PRFS = cows that conceived to their first service; NIC = cows not in calf at end of the breeding season; CR21 = cows that calved in the first 21 d from the planned start of the calving; CR42 = cows that calved in the first 42 d from the planned start of the calving. All heritability and repeatability estimates were significantly different from zero ( $P < 0.001$ ).

populations. The superiorities of milk production yields in F cows were higher in TAD, being twice as high as in the OAD milking system, but J cows had greater FP, PP, and LP than F cows in both milking systems. The highest individual breed effect was found with MY followed by LY, PY, and FY in both OAD and TAD, respectively. In both milking populations, individual breed effects for fertility traits were found to be in favor of J cows. Results indicated that J cows in OAD milking population had significantly shorter SMFS (<1.2 d), SMCO (<1.5 d), FSCO (<0.5), CFS (<1.2 d), and CInt (<1.1 d), and significantly higher proportions of SR21 (>2.0%), SR42 (>1.8%), PR21 (>3.9%), PR42 (>2.9%), PRFS (>3.6%), CR21 (>3.5%), and CR42 (>1.9%) than F cows. Likewise, in the TAD population, J cows were superior for fertility traits, having significantly shorter SMFS (<1.8 d), SMCO (<2.3 d), CFS (<1.8 d), and CInt (<1.7 d), and significantly higher proportions of SR21 (>6.9%), SR42 (>3.8%), PR21 (>4.6%), PR42 (>3.1%), CR21 (>4.0%), and

CR42 (>2.5%) than F cows. Estimates for the individual breed effects for SMFS and CFS were similar within the OAD and TAD populations.

Crossbred F × J cows produced significantly higher MY, FY, PY, LY, and LP than the average of the parental breeds under both milking regimens. Individual heterosis effects for fertility favored F × J cows in such a way that they had significantly fewer days from SMFS, SMCO, FSCO, CFS, and CInt; significantly higher proportions of SR21, SR42, PR21, PR42, PRFS, CR21, and CR42; and a lower proportion of NIC than the averages of parental breeds in both milking systems. In general, individual heterosis effects for fertility traits were similar across the milking populations, but heterosis effects for PR42, CR21, and CR42 tended to be greater in magnitude in the TAD milking population compared with the OAD milking population.

Estimates of the individual recombination loss effects were significant and favorable for FY, PY, FP, and

**Table 5.** Individual and maternal breed, heterosis effects, and individual recombination loss coefficients<sup>1</sup> (SE) for production and fertility traits of Holstein Friesian (F), Jersey (J), and crossbred of Holstein Friesian and Jersey (F × J) cows milked once daily and twice daily

Trait	Once-daily milking					Twice-daily milking				
	F - J <sup>I</sup>	$h_{F \times J}^I$	r <sup>I</sup>	F - J <sup>M</sup>	$h_{F \times J}^M$	F - J <sup>I</sup>	$h_{F \times J}^I$	r <sup>I</sup>	F - J <sup>M</sup>	$h_{F \times J}^M$
<b>Production<sup>2</sup></b>										
MY	869.6 (35.5)***	196.7 (16.2)***	-23.5 (23.1)	-111.3 (22.0)*	19.62 (12.1)	1,397 (26.3)***	235.1 (11.0)***	-80.9 (55.0)***	-108.6 (15.8)**	27.3 (16.6)***
FY	8.56 (1.76)***	12.73 (0.81)***	9.57 (3.62)***	-2.10 (1.11)	-0.57 (1.14)	13.22 (1.24)***	16.22 (0.53)***	9.35 (2.56)***	-2.04 (0.75)	-1.87 (0.78)**
PY	20.42 (1.39)**	9.08 (0.65)**	6.13 (1.36)**	-3.48 (0.87)**	1.07 (0.48)	31.16 (0.90)***	11.04 (0.39)**	6.05 (1.87)*	-1.89 (0.55)	-1.15 (0.57)
LY	40.89 (1.85)***	10.52 (0.85)***	-1.61 (1.20)	-5.02 (1.15)	1.20 (0.63)*	66.4 (1.37)***	12.79 (0.57)***	-10.35 (1.27)***	-4.91 (0.82)	0.83 (0.86)***
FP	-1.06 (0.04)***	-0.01 (0.02)	0.25 (0.03)***	0.04 (0.02)*	0.004 (0.01)**	-1.12 (0.02)***	-0.02 (0.01)	0.14 (0.04)***	0.03 (0.01)*	-0.05 (0.01)***
PP	-0.43 (0.02)***	0.0004 (0.01)	0.01 (0.01)	0.005 (0.01)*	0.001 (0.01)**	-0.49 (0.01)***	0.001 (0.003)	0.13 (0.02)***	0.03 (0.005)	-0.03 (0.01)***
LP	-0.08 (0.01)***	0.01 (0.005)**	-0.02 (0.01)	0.02 (0.01)***	0.01 (0.003)*	-0.06 (0.01)***	0.02 (0.002)***	0.05 (0.01)*	-0.002 (0.003)*	-0.01 (0.003)*
<b>Fertility<sup>3</sup></b>										
SMFS	1.16 (0.39)***	-0.80 (0.25)***	-0.17 (0.42)	0.12 (0.29)	-0.24 (0.18)	1.77 (0.25)***	-0.90 (0.13)***	-0.34 (0.49)**	-0.09 (0.17)	0.04 (0.16)*
SMCO	1.49 (0.97)**	-3.04 (0.63)***	-1.60 (1.07)	-1.27 (0.74)	-0.46 (0.46)	2.03 (0.67)**	-4.29 (0.34)***	-3.25 (1.33)*	-0.13 (0.44)	0.58 (0.44)
FSCO	0.52 (0.74)*	-2.10 (0.50)***	-0.79 (0.85)	-0.96 (0.58)	-0.08 (0.37)	-0.25 (0.51)	-2.81 (0.27)***	-2.53 (0.98)***	-0.18 (0.35)	0.59 (0.33)*
CFS	1.16 (0.39)***	-0.80 (0.25)***	-0.17 (0.42)	0.12 (0.29)	-0.24 (0.18)	1.77 (0.25)***	-0.89 (0.13)***	-0.31 (0.48)**	-0.08 (0.17)	0.04 (0.16)*
CInt	1.14 (0.65)*	-1.86 (0.44)***	0.56 (0.74)	-0.88 (0.51)*	0.02 (0.32)	1.74 (0.43)***	-1.94 (0.23)***	-0.81 (0.82)	-0.68 (0.29)**	-0.05 (0.28)
SR21 (%)	-1.97 (1.26)*	2.80 (0.78)***	-1.11 (1.31)	-0.40 (0.94)	0.45 (0.57)	-6.87 (0.79)***	3.08 (0.40)***	-1.21 (1.56)***	0.93 (0.52)*	0.54 (0.51)**
SR42 (%)	-1.75 (0.81)***	1.15 (0.51)*	0.15 (0.86)*	-0.42 (0.61)	1.01 (0.37)	-3.75 (0.46)***	1.50 (0.25)***	-0.60 (0.88)**	0.22 (0.32)	0.20 (0.30)*
PR21 (%)	-3.92 (1.68)***	5.49 (1.13)***	1.65 (1.92)	3.55 (1.32)**	-0.43 (0.83)	-4.59 (0.99)***	5.84 (0.52)***	1.88 (1.95)	1.62 (0.67)*	-0.51 (0.65)
PR42 (%)	-2.87 (1.46)***	4.12 (0.96)***	2.62 (1.63)	2.25 (1.13)*	0.68 (0.71)	-3.12 (0.95)***	5.79 (0.49)***	4.46 (1.87)*	0.11 (0.64)	-1.01 (0.62)
PRFS (%)	-3.56 (1.61)***	3.15 (1.11)***	3.60 (1.89)	3.52 (1.28)*	-0.44 (0.81)	-0.24 (0.95)	3.70 (0.53)***	1.86 (1.78)	1.02 (0.67)	-0.54 (0.63)
NIC (%)	0.19 (1.01)	-2.32 (0.68)***	-3.03 (1.15)	-0.81 (0.79)	-0.62 (0.50)	1.69 (0.69)*	-3.25 (0.36)***	-1.97 (1.35)*	0.34 (0.47)	0.41 (0.45)
CR21 (%)	-3.49 (2.14)*	2.89 (1.45)*	-0.45 (2.44)	4.13 (1.66)**	-0.59 (1.05)	-4.00 (1.22)***	4.08 (0.72)***	-0.69 (2.19)	1.91 (0.87)*	0.16 (0.80)
CR42 (%)	-1.93 (1.45)*	1.57 (1.00)	2.13 (1.70)	3.15 (1.14)**	0.88 (0.72)	-2.45 (0.95)**	2.81 (0.57)***	-0.48 (1.71)	0.62 (0.68)	-0.31 (0.63)

<sup>1</sup>F - J<sup>I</sup> = individual breed effect;  $h_{F \times J}^I$  = individual heterosis effect represents the difference between the average of reciprocal first crosses and the average of straightbred dams of cows;  $r^I$  = individual recombination loss coefficient; F - J<sup>M</sup> = maternal breed effect;  $h_{F \times J}^M$  = maternal heterosis effect represents the difference between the average of reciprocal first crosses and the average of straightbred dams of cows.

<sup>2</sup>MY = milk yield (kg); FY = fat yield (kg); PY = protein yield (kg); LY = lactose yield (kg); FP = fat percentage; PP = protein percentage; LP = lactose percentage.

<sup>3</sup>SMFS = 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); CInt = consecutive calving interval (d); SR21 = cows inseminated in the first 21 d from the start of mating; SR42 = cows inseminated in the first 42 d from the start of mating; PR21 = cows conceived in the first 21 d from the start of mating; PR42 = cows conceived in the first 42 d from the start of mating; PRFS = cows that conceived to their first service; NIC = cows not in calf at end of the breeding season; CR21 = cows that calved in the first 21 d from the planned start of the calving; CR42 = cows that calved in the first 42 d from the planned start of the calving.

\*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001.

SR42 in OAD. In the TAD milking population, individual recombination loss effects were significant for all production traits, but estimates were favorable for FY, PY, and milk composition traits. Individual recombination loss estimates were significant and unfavorable for SR21 and SR42 in the TAD milking population, although effects were slightly favorable and significant for SMFS, SMC0, FSCO, CFS, PR42, and NIC in the TAD milking population. In general, most of the estimated recombination loss effects were relatively small compared with heterosis effects, and recombination effects were less likely to be significant for production and fertility traits in OAD.

### **Maternal Breed, Heterosis, and Recombination Effects**

The estimates of maternal breed effects for milk production traits were in the opposite direction to the individual maternal breed effects. Maternal breed effects for MY, PY, FP, PP, and LP were significant in OAD milking, whereas maternal breed effects of MY, FP, and LP were significant in TAD milking system. Although individual breed effects for FP, PP, and LP were in favor of J cows in both milking populations, maternal breed effects for FP, PP, and LP were in favor of F dams. Maternal breed effects were also significant for CInt, PR21, PR42, PRFS, CR21, and CR42 in OAD and for CInt, SR21, PR21, and CR21 in TAD, and these effects were in favor of the F dam.

In both milking populations, maternal heterosis effects for yield traits were similar, and maternal heterosis effects for FP, PP, and LP were closer to zero. Maternal heterosis effects for LY, FP, PP, and LP were significant in OAD. Thus, daughters of crossbred F × J dams had more LY (1.2 kg) and higher FP (0.004%), PP (0.001%), and LP (0.01%) than the average performances of their parental breeds in the OAD milking system. For the TAD milking cow population, estimates of maternal heterosis effects for MY, FY, LY, FP, PP, and LP were also significant; daughters of crossbred F × J dams produced 27 kg more MY, 1.9 kg less FY, 0.83 kg more LY, and less FP (−0.05%), PP (−0.03%), and LP (−0.01%) compared with the average performances of purebred F and J dams. In general, maternal heterosis effects for fertility traits were not significant in OAD; however, significant maternal heterosis effects were observed with SMFS, FSCO, CFS, SR21, and SR42 in the TAD milking population. Most of the maternal recombination effects for production and fertility traits were not significant in either milking population (results not presented).

## **DISCUSSION**

### **Production and Fertility Performances**

The means of MY, FY, PY, FP, PP, CInt, SR21, PR42, and PRFS were similar to the national averages reported for 3 seasons from 2015–2016 to 2017–2018 in New Zealand (LIC and DairyNZ, 2021). As reported by Hemming et al. (2018) and Edwards (2018), we found that cows milked OAD for the entire lactation had improved reproductive performance, in terms of the higher means of SR21, PR42, PRFS, and CR42 and lower NIC than cows milked TAD. The improved reproductive performance in OAD milking cows is likely due to the improved energy balance in the early lactation of cows milked OAD compared with TAD (Phyn et al., 2010; Kay et al., 2013; Phyn et al., 2014).

### **Variance Components, Heritability, and Repeatability Estimates**

The greater variance components for production traits in the TAD population compared with the OAD population may result from the greater milk production in this population. Nevertheless, the heritability and repeatability estimates for production traits were similar in both milking populations, which could be due to the scale effect.

In general, heritability estimates for yields and milk composition traits were found to be within the range reported in the literature (MY, FY, PY, and LY: 0.16–0.36; FP, PP, and LP: 0.35–0.67) in cows milked TAD in New Zealand (Ahlborn and Dempfle, 1992; Bryant et al., 2007; Lembeye et al., 2016; Lopez-Villalobos et al., 2020). Heritabilities of MY, FY, PY, FP, and PP in OAD milking population in this study are consistent with the findings of Lembeye et al. (2016) in New Zealand. As far as we are aware, this is the first study to estimate genetic parameters for LY and LP in cows milked OAD.

Estimates of heritability for LY were slightly higher than the estimates of heritability for FY and PY in both milking populations. The main export dairy products of New Zealand are whole (WMP) and skim milk powder (SMP), cheese, butter, and casein (Sneddon et al., 2016). The standardization of milk for WMP and SMP requires the 3 main milk components (fat, protein, and lactose) to meet specified codex standards. Sneddon et al. (2016) showed that if the milk from the average New Zealand cow was manufactured without standardization, the WMP produced is lower in lactose than the required composition. To address this dispar-

ity, milk processing companies can purchase lactose to fill the lactose deficit. Sneddon et al. (2016) demonstrated that including LY in the selection index would produce genetic responses toward a milk more suitable for WMP and SMP. Table 2 shows that milk produced from OAD milking cows is higher in FP and PP than milk from TAD milking cows. The economic value of selection for lactose in OAD milking cows needs to be estimated to determine whether LY should be included in OAD selection indexes.

The low heritabilities of SMFS, SMCO, FSCO, CFS, and CInt in both OAD and TAD populations in this study agree with previously published estimates for TAD populations in New Zealand, British, Irish, and Australian dairy cattle populations (ranging between 0.01 and 0.07; Grosshans et al., 1997; Pryce et al., 1998; Kelleher et al., 2016; Morton et al., 2018). The New Zealand dairy production system depends on a seasonal calving pattern. Measuring fertility using interval traits, as from calving to the event (CFS, CInt), can be biased due to differences in the interval from calving to start of the mating season for early- versus late-calving cows. In New Zealand, the mating season starts on a fixed calendar date, meaning cows that calve early have a longer interval from calving to the start of mating than cows that calve later. For this reason, the 2 key fertility metrics used in New Zealand are SR21 and PR42. Dairy farmers aim to maintain a 365-d calving interval by minimizing the interval between the start of mating and first service and maximizing the proportion of cows that conceive within 42 d of the start of mating.

Heritability estimates for SR21 and CR42 have been well reported in the New Zealand dairy cattle population (Pryce and Harris, 2006; Bowley et al., 2015; Craig et al., 2018). However, genetic parameters for SR42, PR21, PR42, PRFS, and CR21 are not typically reported. Heritability estimates for SR21 and CR42 in this study are consistent with previously cited studies in New Zealand (SR21: 0.01–0.07 and CR42: 0.01–0.029). Heritabilities of PR42 and NIC tended to be slightly higher in TAD than OAD milking cows, but no other studies have reported heritability for NIC in New Zealand for comparison. Morton et al. (2018) reported 0.04 heritability for PR42 and NIC in Australian dairy cattle, similar to the present results. In general, the low heritabilities of fertility traits are a consequence of small genetic variation and relatively large residual variation in both milking systems, which means that management, feeding, and environmental factors have a greater influence on reproductive performance than genetic factors.

The similar repeatabilities among OAD and TAD populations for milk yield and milk composition were

consistent with previous comparisons of genetic parameters for OAD and TAD production traits in New Zealand (Sneddon et al., 2015a; Lembeye et al., 2016; Lopez-Villalobos et al., 2020). There is a paucity of published estimates of repeatability for fertility traits. The similarities in repeatability of fertility traits between OAD and TAD populations reported here means that inference can likely be made for OAD populations from future studies involving TAD populations.

### **Individual Breed, Heterosis, and Recombination Effects**

In general, breed effects on milk production agree with published estimates (Ahlborn-Breier and Hohenboken, 1991; Lembeye et al., 2015; Sneddon et al., 2015a). Holstein Friesian cows produced the greatest volumes of milk in both OAD and TAD herds. Breed effects for FY and PY in the OAD milking population were relatively smaller than in the TAD milking population. This is likely due to a scale effect, as cows milked OAD produced less milk than cows milked TAD. Breed effects were negative for percentages of milk components, which agrees with the findings of Sneddon et al. (2015b), who reported that J cows produced less milk volume but higher concentrations of fat and protein. Breed effects for FP and PP were slightly greater in TAD than in OAD milking and were small for LP in both OAD and TAD. In an experimental study, Clark et al. (2006) found no significant breed and milking frequency interaction for milk compositional traits.

In agreement with the current results, studies in the United States (Washburn et al., 2002), Ireland (Prendiville et al., 2011), and Denmark (Freyer et al., 2008) have reported that J cows milked TAD had better reproductive performance than F cows. As was the case in the current study, Clark et al. (2006) reported J cows milked in both OAD and TAD had higher SR21 than F cows in New Zealand. McClearn et al. (2020) suggested that F herds with poor fertility performance and low milk fat and protein percentages are likely to benefit considerably from crossbreeding with J, and all herds are likely to benefit in terms of production efficiency.

The significant heterosis effects observed for MY, FY, and PY for OAD and TAD milking systems in this study agree with the estimates reported by Lembeye et al. (2015). These estimates tended to be greater in TAD than in OAD milking cows. The magnitude of the heterosis effect for first-cross F × J cows in the TAD system in our study were greater than the findings of Harris (2005), who reported heterosis for MY, FY, and PY as 139 kg, 7.7 kg, and 5.5 kg, respectively. A possible reason for this difference is that milk production

has increased over time. Average milk, milk fat, and protein production per cow in the national herd has increased by 577 kg, 31 kg, and 29 kg from production seasons 2004–2005 to 2017–2018 (LIC and DairyNZ, 2021).

In New Zealand, studies by Harris and Kolver (2001) and Harris et al. (2006) reported that first-cross F × J cows had 1.5-d shorter SMFS, 10.1% greater pregnancy rate, 4.3% greater SR21, and 3.4% greater CR42 compared with the mean performances of the parental F and J breeds. We found favorable heterosis effects for SMFS, 3-wk and 6-wk pregnancy rates, SR21 and CR42 with F × J cows in both milking systems. However, the magnitude of the effects is slightly lower in the present study compared with previous works. In agreement with our findings, favorable heterosis effects were reported for CFS, CInt, SR21, and PR42 in crossbred Holstein × Jersey and Holstein × Friesian cows in Irish and British dairy cattle populations (Wall et al., 2005; Kelleher et al., 2016; CFS: −1.1 d; CInt: −1.6 d to −9 d; SR21: 4%; and PR42: 6%).

Estimated breed effects for fertility traits tended to be greater in TAD than OAD in this study. Although phenotypic reproductive performance is already better in OAD than TAD herds, heterosis effects through the use of crossbred cows offer the potential to increase phenotypic performance in both milking systems. Heterosis effects for fertility traits were similar in both milking populations except for 6-wk in-calf and calving rates, indicating positive effects of heterosis on fertility in both milking systems.

There is a paucity of information available in literature for recombination effects of production and fertility traits of crossbred cows in New Zealand. Recombination effects estimated in the present study were small and were a mix of favorable and unfavorable effects for production and fertility traits. Although significant and favorable recombination effects were observed, the standard errors of these estimates were high. We suggest these estimates should be used with caution when designing breeding programs using crossbreeding. Further research in this area needs to be conducted.

Large negative recombination effects were found for MY in the TAD milking population, indicating that much of the F<sub>1</sub> heterosis for MY was lost in advanced backcrosses or second crossbred cows. However, recombination effects for FY and PY in both milking populations were positive. This indicates that farmers using crossbreeding systems such as back crossing, 2-breed rotational crosses or the use of crossbred sires will still benefit from favorable heterosis and recombination effects. The use of crossbred sires is a popular breeding strategy in New Zealand. Over 30% of inseminations use semen from crossbred sires (LIC and DairyNZ, 2021).

In both milking populations, milk composition traits had relatively small heterosis and recombination loss effects, implying that these traits are more influenced by additive genetic effects rather than interactions between alleles in the same locus or different loci. There is conflicting evidence for the direction of recombination effects in the literature. VanRaden and Sanders (2003) reported slightly favorable recombination for yields in US dairy herds. In contrast, Dechow et al. (2007) and Dezetter et al. (2015) reported unfavorable recombination effects for production and fertility traits. In the current study, most recombination effects were not significant in the OAD milking population, whereas estimated recombination effects were significant but small in the TAD milking population. Heterosis effects have a greater potential than recombination effects to improve production efficiency on-farm.

### Maternal Breed and Heterosis Effects

Maternal breed effects in favor of J dams for MY and F dams for FP in both milking populations are consistent with previous research. Ahlborn-Breier and Hohenboken (1991) reported 51 kg of MY in favor of the J dams and 0.1% of FP in favor of F dams in the TAD milking system. Similarly, the low but significant maternal heterosis effect for FP in the TAD milking system is similar to the −0.05% reported by Ahlborn-Breier and Hohenboken (1991).

Our results show that maternal heterosis effects for fertility traits were not significant in OAD milking population, suggesting that maternal heterosis has a lesser effect on cow fertility in OAD milking system. To our knowledge, no previous study has investigated the maternal breed and heterosis effects for fertility traits in New Zealand; therefore, no estimates are available in the present literature to compare our findings. Interestingly, our results indicate that daughters of crossbred F × J dams had a significantly higher SR21 and SR42 than the average performance of purebred F and J dams, although they had significantly longer SMFS, FSCO and CFS in the TAD milking system. The reasons for unfavorable maternal heterosis effects on SMFS, FSCO, and CFS have not been identified in this study.

At present, crossbred F × J cows account almost half of the national herd in New Zealand. The reason for the rapid increase of numbers of crossbred cows in the national herd is due to their better production efficiency, fertility, and improved health and survival (Montgomerie, 2005). Lopez-Villalobos et al. (2000) simulated the profitability of crossbreeding systems and found that a herd using a 2-breed rotational crossbreeding with F and J breeds showed superior farm

profitability compared with straightbred herds. Clasen et al. (2020) used the phenotypic breed and heterosis effects to simulate the profitability of crossbreeding in 2 different production systems of organic and conventional herds in Sweden. Similarly, breed and heterosis effects reported for production and fertility traits in this study can also be used in simulation studies to design optimal crossbreeding strategies for OAD and TAD milking production systems.

## CONCLUSIONS

The present study provided heritability and repeatability estimates for production and fertility traits of the OAD milking cow population in New Zealand. Individual and maternal heterosis and recombination losses were also estimated. Reported heritability and repeatability estimates in cows milked OAD were broadly similar to those of TAD milking cows. Importantly, most of the individual breed and heterosis effects for production and fertility traits were significant in both milking populations. The maternal heterosis effects for fertility traits of SMFS, FSCO, CFS, SR21, and SR42 were significant in cows milked TAD, but not in cows milked OAD. Recombination effects estimated in the present study were small and showed a mix of favorable and unfavorable effects for production and fertility traits. The adoption of crossbreeding offers an opportunity for those farmers who are not already benefiting from heterosis to reap the benefits of improved milk production and fertility with minimal recombination loss.

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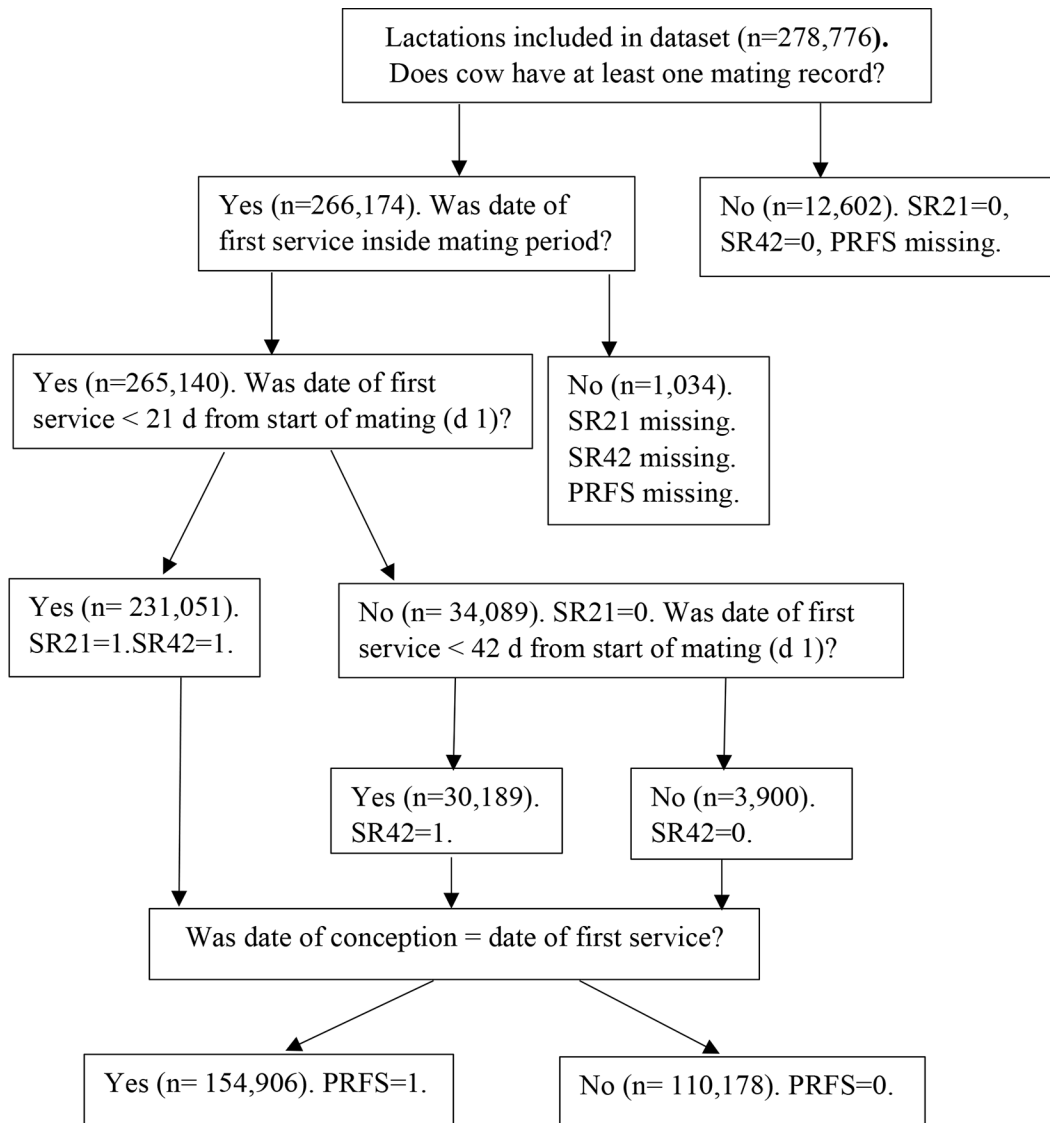
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## APPENDIX



**Figure A1.** Flowchart detailing determination of 3-wk submission (SR21), 6-wk submission (SR42), and conception to the first service (PRFS).