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Genetic Analysis of Postpartum Measures of Luteal Activity in Dairy Cows

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ABSTRACT

The objective of this study was to estimate genetic parameters for measures of luteal activity during the first 60 d postpartum. Analyses were made with different sampling intervals to investigate the possibility of combining progesterone measurement with routinely performed milk recording. Progesterone level in milk as an indicator of female fertility when selecting sires in a progeny-testing scheme was also examined. Data were collected from 1996 to 1999, and comprised 1,212 lactations from 1,080 British Holstein-Friesian cows at 8 commercial dairy farms in the United Kingdom. Milk samples for progesterone analysis were collected thrice weekly. Mixed linear animal models were used to analyze the data. Heritability for the percentage of samples with luteal activity during the first 60 d postpartum (**PLA**) was 0.30 and decreased with more infrequent sampling to 0.25, 0.20, and 0.14 for weekly, twice-monthly, and monthly sampling, respectively. Measures of PLA had a high negative genetic correlation with prolonged anovulation (−0.53 for monthly sampling, < −0.87 otherwise) and a moderate positive genetic correlation with persistent corpus luteum in the first estrus cycle (>0.65 if at least twice-monthly sampling). Genetic correlations with interval from calving to commencement of luteal activity were close to −1 for all PLA measurements and the selection index calculations showed that monthly progesterone sampling could be used with high accuracy (0.80 with 50 daughters per bull) to predict breeding values for commencement of luteal activity. Progesterone analysis at the time of regular milk recording could thereby be used to select for an early interval from calving to commencement of luteal activity and, at the same time, a decreased frequency of prolonged anovulation during the postpartum period.

Key words: luteal activity, fertility, dairy cow, heritability

INTRODUCTION

In recent years there has been an increasing awareness of the need to include fertility in breeding programs (Darwash et al., 1999; Royal et al., 2000a, 2002a; Jorjani, 2005) because of the declining fertility of dairy cows observed in several countries. Royal et al. (2000b) reported a decrease of 1% per year in pregnancy rate to first AI between 1975 and 1998 in the United Kingdom. During this period, pregnancy rates to first service fell to an all-time low of 39.7% and calving interval increased from 12.2 to 12.8 mo. In the United States, Lucy (2001) reported an increase in number of inseminations per conception from 1.8 in 1970 to 3.0 in 1999, and an increase in calving interval from 13.5 to 14.7 mo. In Sweden, the calving interval increased from 12.6 mo in 1974 and 1975 to 13.3 mo in 2004 and 2005 (Swedish Dairy Association, 2005).

Fertility has been included in Nordic breeding programs for dairy cattle since the early 1970s (Lindhé et al., 1994). However, the genetic trend has shown a decrease in fertility of Swedish Holsteins whereas the genetic level has been relatively constant for the Swedish Red (Lindhé and Philipsson, 2001). It seems that inclusion of fertility in the breeding goal in Sweden has not been enough to withstand the effects of importation of genetic material into the Swedish Holsteins from countries that have a low, or no, weighting on fertility in their breeding objective. The traits traditionally used in the genetic evaluation for fertility (e.g., number of inseminations per service period and interval between calving and first AI) have very low heritabilities (Roxström et al., 2001; Wall et al., 2003). This may be partly a result of the large influence of management on the measurements that are used in present breeding pro-

grams for fertility. For instance, the rationale for measuring the interval from calving to first AI (**CFI**) is to obtain an indirect measure of interval from calving to first ovulation (**CFO**). However, CFI is affected by the farmer's decision of when to start the service period, which may vary between herds and between cows within herds.

In recent studies (Darwash et al., 1997a; Royal, 1999; Veerkamp et al., 2000; Royal et al., 2002a), a measure more related to CFO has been presented, namely the interval from calving to commencement of luteal activity (**C-LA**). The definition of C-LA is the interval from calving until the progesterone level in milk reaches a threshold value, thereby indicating progesterone production by the corpus luteum. The occurrence of C-LA is about 4 to 5 d after first ovulation (Darwash et al., 1997a) and is thereby a direct measurement of the resumption of ovarian activity after calving. In these studies of C-LA, heritability estimates of 16 to 21% have been reported, which is considerably higher than for traditional measurements of fertility in dairy cows.

At a phenotypic level, early onset of estrus cyclicity increases the probability of an early insemination after calving, shortens the interval from calving to conception, increases conception rate, and reduces the number of services per conception (Darwash et al., 1997b). Furthermore, at a genetic level, cows with genetically longer C-LA on average have longer calving intervals and longer interval to first service (genetic correlations of 0.39 and 0.53, respectively; Royal et al., 2003). However, not only is the time until first ovulation (reflected by C-LA) important for fertility in dairy cows, but so is the subsequent progesterone pattern. Different aberrations in progesterone profiles are associated with a longer CFI, longer interval from calving to conception, and lower pregnancy rates (Royal et al., 2000a; Petersson et al., 2006a). The decreasing trend in pregnancy rates at first AI in the study from the United Kingdom was accompanied by an increase from 32 to 44% in atypical progesterone profiles, especially those with a prolonged luteal phase (Royal et al., 2000b). We have previously shown that by using the percentage of samples taken within the first 60 d after calving with luteal activity (i.e., progesterone ≥3 ng/mL; **PLA**), we can separate not only profiles with delayed onset of ovarian activity from normal profiles (as does C-LA) but also profiles with prolonged luteal phase from normal profiles (Petersson et al., 2006a).

In studies of C-LA, progesterone samples were taken relatively frequently (2 to 3 times a week; Darwash et al., 1997a; Royal, 1999; Veerkamp et al., 2000; Royal et al., 2002a; Petersson et al., 2006b). For use in a breeding program, such frequent sampling would require an online progesterone monitoring system. How-

ever, it will probably be many years until all dairy herds are equipped with such systems. An alternative would be to use milk samples from the routine milk recording for analysis of progesterone (Darwash et al., 1999; van der Lende et al., 2004). The disadvantage is that these samples are taken relatively infrequently (once a month), and it needs to be determined how sampling frequency affects the interpretation of different progesterone profiles as well as how it affects the genetic parameters of progesterone-based measurements.

The objective of this study was to investigate the possibility of combining progesterone sampling with routinely performed milk recording. Therefore, genetic parameters for a trait based on measures for luteal activity during the first 60 d postpartum (PLA) were estimated with different sampling intervals. Consequences for incorporating PLA in breeding programs for fertility in dairy cattle are discussed.

MATERIALS AND METHODS

Data

For this study we utilized a milk progesterone database from the University of Nottingham and Roslin Institute that has been studied previously (Royal, 1999; Royal et al., 2000b, 2002a,b, 2003). Additional information from 2 commercial databases—National Milk Records Plc (**NMR**; Chippenham, UK) and Holstein United Kingdom (**HUK**; Ricksmanworth, UK)—was also included. Data for the milk progesterone database were collected between October 1996 and March 1999, and comprised 1,212 lactations from 1,080 cows in 8 herds. Pedigrees with 3 generations were created with information from the HUK database for all cows in the study. The average paternal half-sib family size was 6.4 daughters, and the distribution of half-sib family sizes has been illustrated previously (Royal et al., 2002a). Milk records were obtained from the NMR database or directly from Roslin Institute. For analysis of milk yield, predicted 56-d milk yield (**MY56**) was used, as calculated in Royal et al. (2002a). North American Holstein percentage (**PCH**) of cows and bulls were taken from the HUK database, where available, or calculated from known pedigrees using information on sire and origin of maternal ancestors. Distribution of PCH for cows and sires has been illustrated earlier (Royal et al., 2002a). Percentage Holstein and percentage Friesian were used to calculate expected percentage heterosis (**HET**) as $P_{Dam} (1 - P_{Sire}) + P_{Sire}(1 - P_{Dam})$, where P represents percentage Holstein. Percentage heterosis was added to the analysis to account for a simple, nonadditive genetic effect.

Milk progesterone samples were taken 3 times per week (Mondays, Wednesdays, and Fridays) from 2 to 8

d postpartum until a maximum of 24 d after the first AI (for further details, see Royal et al., 2000a). Progesterone concentration was measured in unextracted samples of whole milk using ELISA (Ridgeway Science Ltd., Alvington, UK). The intraassay coefficients of variation, calculated using a representative sample of 100 assays, for control standards at 2 and 8 ng/mL were 0.129 and 0.060, respectively. The interassay coefficients of variation for 2 and 8 ng/mL were 0.127 and 0.081, respectively. Sensitivity was 1 ng/mL, calculated using the absorption of the blank standard minus 2 standard deviations.

The occurrence of estrus was recorded. Where possible, in addition to visual routine checks by the herdsman, heat mount detectors (Kamar Inc., Steamboat Springs, CO) were used. Treatment of reproductive disorders was withheld for 80 d after calving unless required for welfare reasons. Data concerning 44 animals that received hormone treatment of reproductive disorders before insemination were removed from selected analyses, where appropriate. The incidence of dystocia, retained placenta, and uterine infection was recorded. However, only uterine infection was included as a covariate in this study, as no effects of dystocia and retained placenta on the studied fertility measures were found in preliminary analyses of the data.

Fertility Measurements

Interval from calving to C-LA was defined as the number of days from calving until the day of the first of 2 consecutive milk progesterone concentrations ≥3 ng/mL. Furthermore, the PLA (progesterone ≥3 ng/mL) was calculated for all or a subset of samples taken within 60 d after calving (Petersson et al., 2006a,b). For the definition of **PLA$_a$** all samples in the current database (3 per week) was used for the calculation. For PLA based on weekly sampling (**PLA$_w$**), only the first sample in each week was included. For PLA based on sampling twice a month (**PLA$_f$**), only the first sample in every 2-wk period was included. For PLA based on random monthly sampling (**PLA$_m$**), a sample within the first 4 wk of lactation was randomly chosen, utilizing SAS procedure SURVEYSELECT (SAS Institute, 2001). For this measure, the first sample together with the sample taken 4 wk later was used.

The progesterone profiles, constructed using the milk progesterone samples, were used to classify different ovarian patterns using definitions published by Lamming and Darwash (1998). Delayed ovulation type 1 (**DOV1**) was defined as prolonged anovulation postpartum with milk progesterone <3 ng/mL for ≥45 d after calving. Delayed ovulation type 2 (**DOV2**) was defined as prolonged interluteal interval with milk progesterone

one <3 ng/mL for ≥12 d between 2 luteal phases. Persistent corpus luteum type 1 (**PCL1**) was defined as delayed luteolysis with milk progesterone ≥3 ng/mL for ≥19 d during the first postpartum estrous cycle. Persistent corpus luteum type 2 (**PCL2**) was defined as delayed luteolysis with milk progesterone ≥3 ng/mL for ≥19 d during estrus cycles after the first cycle.

Statistical Analysis

The REML option of the DMU package (Jensen and Madsen, 1994) was used to fit a mixed linear animal model to the data. The following model was used for the analyses:

$$y_{mnopqrstuv} = \mu + l_m + h_n + yr_o + s_p + ui_q$$
$$+ d_r + b_1pch_s + b_2het_t + hys_{nop} + a_u + e_{mnopqrstuv}$$

where $y_{mnopqrstuv}$ is the analyzed trait; μ is the overall mean; l_m is the fixed effect of lactation number (m = 1 to 9); h_n is the fixed effect of herd (n = 1 to 8); yr_o is the fixed effect of calving year (o = 1995 to 1998); s_p is the fixed effect of season (P = 1 to 4, for December to February, March to May, June to August, September to November); ui_q is the fixed effect of uterine infection postpartum (q = yes or no); d_r is the fixed effect of diet (r = 1 to 23); b_1pch_s is the fixed regression on PCH with coefficient b_1; b_2het_t is the fixed regression on HET with coefficient b_2; hys_{nop} is the random effect of herd-year-season interaction, assumed to be normally distributed with mean zero and variance σ^2_{hys}; a_u is the random effect of breeding value of animals, assumed to be normally distributed with mean zero and variance $\mathbf{A}\sigma^2_A$, where $\mathbf{A}$ is the numerator relationship matrix; and $e_{mnopqrstuv}$ is the random residual term, with residuals assumed to be normally distributed with mean zero and variance σ^2_e. The random effect of permanent environment (effect of cow over lactations) and the random effects of interaction of herd-year, herd-season, and year-season were also tested with likelihood ratio tests; but none of these effects was significant and they were omitted from further analyses. Before inclusion in the mixed linear model, C-LA was transformed (natural logarithm, lnC-LA) because this transformation was shown by Darwash et al. (1997a) to give the best model fit. In the heritability calculations, the herd-year-season variance was not included in the phenotypic variance. Variance components and breeding values were obtained from a single-trait analysis but for correlations, a bivariate analysis was applied.

Estimates of heritabilities and genetic correlations were used for selection index calculations with CFI or lnC-LA in the breeding goal T and CFI or PLA$_m$ or both

Table 1. Definition, number of observations (n), overall mean, standard error (SE), and standard deviation (SD) for C-LA, PLA$_a$, PLA$_w$, PLA$_f$, and PLA$_m$

Measurement	Abbreviation	n	Mean	SE	SD
Interval from calving to commencement of luteal activity (d)	C-LA	1,206	28.5	0.5	17.8
PLA,[1] based on all samples (%)	PLA$_a$	1,209	47.3	0.6	20.7
PLA, based on weekly sampling (%)	PLA$_w$	1,209	44.1	0.6	21.3
PLA, based on twice-monthly sampling (%)	PLA$_f$	1,209	41.3	0.6	22.2
PLA, based on monthly sampling (%)	PLA$_m$	1,169	43.8	1.0	33.8

[1]Percentage of samples with luteal activity during the first 60 d postpartum.

in the index I and maximizing the correlation between T and I, i.e., the accuracy (r_{TI}). For analysis of sensitivity, the genetic correlation between PLA$_m$ and lnC-LA was changed to −0.9 and −0.8. All calculations were done assuming 50 or 100 daughters per bull.

RESULTS

Mean of PLA generally decreased as sampling frequency decreased, going from 47.3% for PLA$_a$ to 41.3% for PLA$_f$ ($P < 0.05$; Table 1). The number of lactations was lower for PLA$_m$ because there had to be a corresponding sample 4 wk after the first randomly chosen sample and this was not the case for some of the lactations in the study.

Table 2 shows the average C-LA and the different PLA measures per type of progesterone profile. The averages of all PLA measurements were generally lower for cows that had a DOV1 or DOV2 and higher for cows that had a PCL1 compared with cows with no atypical progesterone profile (Table 2). Cows with a

DOV1 profile also had a later C-LA than cows with no atypical progesterone pattern. The other atypical progesterone profiles did not have a different mean of C-LA compared with cows with no atypical profile.

Among the PLA traits, the heritability estimate was 29.5% for PLA$_a$ with all samples included, 24.7% for PLA$_w$ with weekly sampling, 20.1% for PLA$_f$ with twice-monthly sampling, and 14.0% for PLA$_m$ with monthly sampling (Table 3). The environmental variance increased with decreased sampling frequency.

The genetic correlations between different PLA measures and other measures of fertility and milk yield are presented in Table 4. Genetic correlations between different PLA measures are not presented because they were all calculated using in part the same original samples and were consequently highly autocorrelated. The genetic correlations for lnC-LA and DOV1 with the PLA measurements were all high and negative (Table 4). Standard errors of the genetic correlations increased with decreased sampling frequency of the PLA measurements. For PLA$_a$, PLA$_w$, and PLA$_f$, there was a high

Table 2. Mean (SE in parentheses) and number of observations for each type of atypical progesterone profile for C-LA, PLA$_a$, PLA$_w$, PLA$_f$, and PLA$_m$

Progesterone profile[1]	n	C-LA (d)	PLA$_a$ (%)	PLA$_w$ (%)	PLA$_f$ (%)	PLA$_m$ (%)
			Measure[2]			
DOV1	184	61.2[a] (1.5)	13.5[a] (0.8)	11.6[a] (0.9)	11.9[a] (1.0)	9.9[a] (1.6)
DOV2	58	23.9[b] (1.7)	39.8[b] (2.4)	37.3[b] (2.6)	35.5[b] (2.7)	41.1[b] (4.2)
PCL1	198	23.9[b] (0.8)	60.2[c] (1.2)	56.5[c] (1.3)	52.6[c] (1.4)	55.9[c] (2.2)
PCL2	90	24.2[b] (1.3)	54.4[cd] (1.9)	51.3[cd] (1.9)	49.6[cd] (2.2)	50.0[bcd] (3.5)
At least one atypical pattern	471	37.2[c] (1.1)	40.5[b] (1.2)	37.6[b] (1.2)	35.6[b] (1.2)	37.3[b] (1.6)
No atypical pattern	738	23.0[b] (0.3)	51.7[d] (0.5)	48.2[d] (0.6)	44.9[d] (0.7)	48.0[bd] (1.2)

[a–d]Different superscript letters indicate significant difference based on confidence interval (2 SE) within columns.

[1]DOV1 = Delayed ovulation, type 1 (0 or 1): prolonged anovulation postpartum with milk progesterone <3 ng/mL for ≥45 d after calving; DOV2 = delayed ovulation, type 2 (0 or 1): prolonged interluteal interval with milk progesterone <3 ng/mL for ≥12 d between 2 luteal phases; PCL1 = persistent corpus luteum, type 1 (0 or 1): delayed luteolysis with milk progesterone ≥3 ng/mL for ≥19 d during the first postpartum estrous cycle; PCL2 = persistent corpus luteum, type 2 (0 or 1): delayed luteolysis with milk progesterone ≥3 ng/mL for ≥19 d during estrus cycles after the first cycle.

[2]C-LA = Interval from calving to commencement of luteal activity (d); PLA$_a$ = percentage of samples with luteal activity the first 60 d postpartum (PLA) based on all samples (%); PLA$_w$ = PLA based on weekly sampling (%); PLA$_f$ = PLA based on twice-monthly sampling (%); PLA$_m$ = PLA based on monthly sampling (%).

Table 3. Phenotypic variance (σ_P^2), genetic variance (σ_A^2), herd-year-season variance (σ_{hys}^2, not included in phenotypic variance), heritability (h^2) and standard error of heritability (SE) for different measurements in the data[1]

Measure	σ_P^2	σ_A^2	σ_{hys}^2	h^2 (%)	SE
PLA_a	364.9	107.7	19.52	29.5	5.8
PLA_w	398.1	98.36	14.76	24.7	5.7
PLA_f	433.7	87.36	28.00	20.1	5.5
PLA_m	1,077	151.1	11.22	14.0	5.5
lnC-LA[2]	0.2925	0.0472	0.0136	16.1	5.0
CFI[2]	1,430	155.9	98.89	10.9	5.1
PFI[2]	0.2268	0.0315	0.0000	13.9	9.0
DOV1	0.1202	0.0245	0.0036	20.3	5.4
DOV2	0.0925	0.0001	0.0001	0.1	7.7
PCL1[2]	0.1410	0.0177	0.0003	12.6	6.0
PCL2	0.1321	0.0109	0.0000	8.3	10.2
MY56[2]	29.03	14.42	5.469	49.7	6.2

[1]PLA_a = Percentage of samples with luteal activity the first 60 d postpartum (PLA) based on all samples; PLA_w = PLA based on weekly sampling; PLA_f = PLA based on twice-monthly sampling; PLA_m = PLA based on monthly sampling; lnC-LA = natural logarithm of interval from calving to commencement of luteal activity; CFI = interval from calving to first AI; PFI = pregnancy to first AI; DOV1 = delayed ovulation, type 1: prolonged anovulation postpartum with milk progesterone <3 ng/mL for ≥45 d after calving; DOV2 = delayed ovulation, type 2: prolonged interluteal interval with milk progesterone <3 ng/mL for ≥12 d between 2 luteal phases; PCL1 = persistent corpus luteum, type 1: delayed luteolysis with milk progesterone ≥3 ng/mL for ≥19 d during the first postpartum estrous cycle; PCL2 = persistent corpus luteum, type 2: delayed luteolysis with milk progesterone ≥3 ng/mL for ≥19 d during estrus cycles after the first cycle; MY56 = estimated milk yield on d 56 postpartum.

[2]Published previously in Royal et al., 2002a.

positive genetic correlation with PCL1 and a moderate negative correlation with MY56. Correlations with CFI were low and with high standard errors, except for the correlation with PLA_m; however, this correlation was not significant.

Breeding values from the single-trait analysis for all sires in the database for DOV1 and PCL1 were plotted against breeding values for PLA_a (Figure 1) to further examine the genetic correlations between PLA_a and these 2 types of atypical progesterone profiles. The regression of DOV1 on PLA_a was linear ($P < 0.001$) with decreasing incidence (lower breeding values) of DOV1 with increasing breeding values for PLA_a. This associated with the strong negative genetic correlation be-

tween these measurements. The moderate positive genetic correlation between PLA_a and PCL1 was associated with a more scattered plot and a flatter regression, indicating that higher breeding values for PLA_a were associated with a small increased incidence (higher breeding values) of PCL1.

The genetic correlation between PLA_m and lnC-LA was unity and affected the results of the selection index calculations. The accuracy (r_{TI}) increased substantially when PLA_m was used as an index trait, compared with when CFI alone was used as an index trait and lnC-LA as the breeding goal trait (Table 5). The selection index calculations were also performed with 2 lower genetic correlations (−0.9 and −0.8) between PLA_m and

Table 4. Genetic correlations (SE in parentheses) between the PLA measures and other measurements of fertility and milk yield[1]

Measure	PLA_a	PLA_w	PLA_f	PLA_m
lnC-LA	−0.974 (0.045)	−1.000 (0.050)	−0.929 (0.083)	−1.000 (0.193)
CFI	−0.027 (0.219)	−0.019 (0.235)	0.028 (0.254)	−0.472 (0.294)
DOV1	−0.932 (0.055)	−0.944 (0.063)	−0.873 (0.092)	−0.533 (0.196)
PCL1	0.662 (0.154)	0.650 (0.168)	0.675 (0.178)	−0.044 (13.9)
MY56	−0.359 (0.124)	−0.339 (0.138)	−0.337 (0.152)	0.016 (0.185)

[1]PLA_a = Percentage of samples with luteal activity the first 60 d postpartum (PLA) based on all samples; PLA_w = PLA based on weekly sampling; PLA_f = PLA based on twice-monthly sampling; PLA_m = PLA based on monthly sampling; lnC-LA = natural logarithm of interval from calving to commencement of luteal activity; CFI = interval from calving to first AI; PFI = pregnancy to first AI; DOV1 = delayed ovulation, type 1: prolonged anovulation postpartum with milk progesterone <3 ng/mL for ≥45 d after calving; PCL1 = persistent corpus luteum, type 1: delayed luteolysis with milk progesterone ≥3 ng/mL for ≥19 d during the first postpartum estrous cycle; MY56 = estimated milk yield on d 56 postpartum.
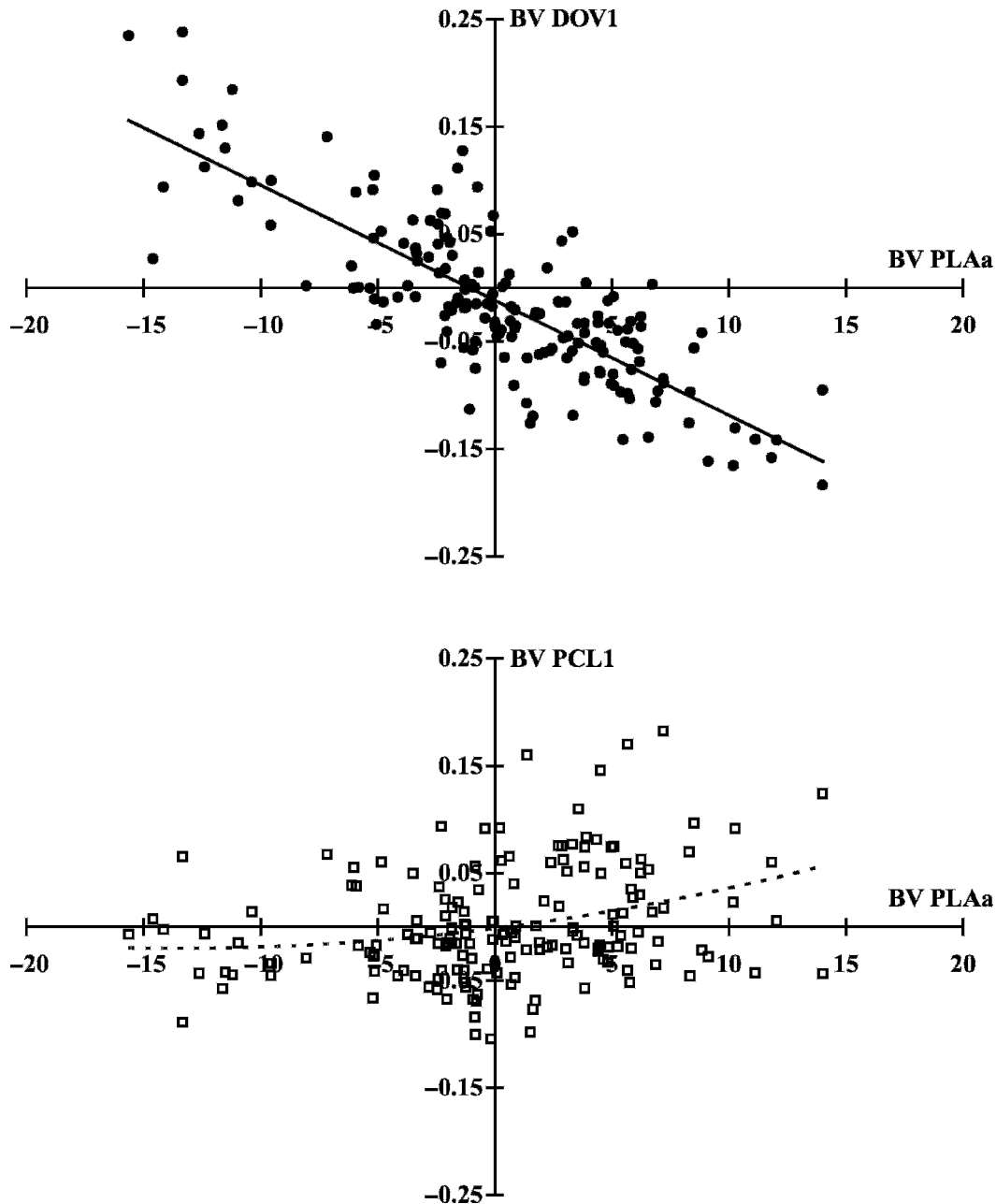
Figure 1. Breeding values (BV) of sires for delayed ovulation, type 1 (DOV1, ●) and persistent corpus luteum, type 1 (PCL1, □) plotted against percentage of samples with luteal activity during the first 60 d postpartum, based on all samples (PLA$_a$). A linear trend-line (——) is shown for DOV1 and a polynomial trend-line (------) for the PCL1.

lnC-LA, which decreased the accuracy by almost 0.1 for each decrease in genetic correlation.

DISCUSSION

The current study examined how infrequent sampling of milk progesterone (e.g., similar to that for regular milk recording) could be used to select for an earlier start of luteal activity after calving in dairy cows. This was performed by studying the percentage of samples with luteal activity in the first 60 d after calving (PLA) with progesterone sampling 3 times per week, weekly, twice monthly, or monthly. The heritability estimates for PLA with these different sampling intervals were high, ranging from 29.5% for the most frequent sampling to 14.0% with monthly sampling.

Table 5. Accuracy (r_{TI}) after selection index calculations with CFI[1] or lnC-LA[2] as breeding goal traits with different index traits and 2 sizes of daughter groups

Index trait(s)	Breeding goal trait	r_{TI} 50 daughters/ bull	100 daughters/ bull
CFI	CFI	0.58	0.71
CFI[3]	lnC-LA	0.09	0.10
PLA$_m$[4]	lnC-LA	0.80	0.88
PLA$_m$ ($r_g = -0.9$)[5]	lnC-LA	0.72	0.80
PLA$_m$ ($r_g = -0.8$)[5]	lnC-LA	0.64	0.71
CFI and PLA$_m$	lnC-LA	0.82	0.92

[1]Interval from calving to first AI.

[2]Natural logarithm of interval from calving to commencement of luteal activity.

[3]Estimated genetic correlation between CFI and lnC-LA was 0.113.

[4]Percentage of samples with luteal activity the first 60 d postpartum, based on monthly sampling.

[5]Calculation with changed genetic correlation between PLA$_m$ and lnC-LA.

We observed a surprisingly high heritability estimate for PLA$_a$ (29.5%) compared with heritability estimates for C-LA found here or previously reported (16 to 21%; Darwash et al., 1997a; Royal et al., 2002a; Veerkamp et al., 2000). The environmental variance of the PLA measures increased with less frequent sampling. This increase in environmental variance was probably partly a result of the decreased number of possible outcomes with decreased sampling frequency; for example, PLA$_m$ had only 3 outcomes: 0, 50, and 100%, because there were only 2 samples in the monthly sampling. The heritability estimates for lnC-LA, CFI, PFI, PCL1, and MY56 have been reported previously (Royal et al., 2002a) and the estimates from the analysis in the present study were in agreement with the earlier study. The unfavorable genetic correlations between MY56 and PLA$_a$, PLA$_w$, and PLA$_f$, respectively, are in accordance with the unfavorable genetic correlation between MY56 and lnC-LA (0.36), as shown by Royal et al. (2002a).

We have previously shown in a Swedish data set that PLA$_a$ could be used to separate DOV1 and a combination of PCL1 and PCL2 profiles from normal profiles (Petersson et al., 2006a). The present study supports this, and the PLA measures (PLA$_a$, PLA$_w$, PLA$_f$, and PLA$_m$) were 33 to 38 percentage points lower for cows with a DOV1 profile and around 8 percentage points higher for cows with a PCL1 profile compared with cows with no atypical profiles. The association between these 2 types of atypical progesterone profiles and PLA was also reflected in the high negative genetic correlations between DOV1 and PLA$_a$, PLA$_w$, and PLA$_f$, respectively, and the moderate to high positive genetic correla-

tion between PCL1 and PLA$_a$, PLA$_w$, and PLA$_f$, respectively. However, these high genetic correlations with PCL1 raise concerns regarding fertility disorders because it has been shown that prolonged luteal phases are associated with pyometra (Etherington et al., 1991). Thus, it appears that there is an intermediate optimum value for PLA: too high a value for PLA is unfavorable because it is associated with PCL1 but a low value could also be unfavorable because it is associated with DOV1. The genetic correlations between PLA$_m$ and DOV1 and PCL1, respectively, indicated that monthly progesterone sampling could give an indication of DOV1 profiles because of the moderate correlation with this type of profiles, but this infrequent sampling regimen cannot be used to detect PCL1 profiles. This low sampling frequency (monthly) was also insufficient to detect the negative genetic correlation that was present between the other PLA measures and MY56. We were not able to estimate genetic correlations between the PLA measures and DOV2 and PCL2 probably due to the low incidence of these 2 types of progesterone profiles.

An alternative measure that has been studied previously is the measurement C-LA50%, introduced by van der Lende et al. (2004), which is the lactation stage when 50% of the daughters of a sire had an active corpus luteum with 3- to 6-wk intervals of progesterone sampling. The basis of C-LA50% is infrequent sampling, as is our PLA$_m$ measurement, but we have applied our measurement on the cow level in contrast to C-LA50%, which was calculated on the sire level. The information obtained on cow level with PLA$_m$ could be used for management purposes; however, this has to be studied further.

Even though the interpretation of PLA is not as straightforward as C-LA, the high genetic correlation with lnC-LA makes it interesting for further analysis. The high negative correlations with lnC-LA could partly depend on the fact that the individuals with the highest breeding values for lnC-LA have the lowest breeding values for the different PLA measures.

A short interval from calving to first ovulation is generally considered desirable. In some breeding programs, CFI is used as an index trait, and used as a breeding goal trait, presumably as a proxy for CFO. Using CFI as the index trait gave an apparent high accuracy when CFI was also used as the breeding goal trait (Table 5). However, C-LA is likely to be a more direct measure of CFO than CFI. There is only a delay of 4 to 5 d between C-LA and CFO, and both C-LA and CFO are determined by the animal's physiology rather than by management practice. Therefore, we suggest using C-LA as the breeding goal trait in a selection index rather than CFI. With C-LA as breeding goal trait in the selection index, PLA$_m$ as index trait resulted in a much higher accuracy

(0.80) compared with when CFI was the index trait (0.09).

Because PLA$_m$ is based on monthly sampling, we concluded that sampling for progesterone at the regular milk recording could be used to increase the accuracy of a breeding program toward an earlier start of cyclical ovarian activity after calving. A breeding program focused only on an earlier C-LA (by selecting on increased PLA) may, however, increase the incidence of progesterone profiles with persistent corpus luteum, because there was generally a positive genetic correlation between the PLA measures and PCL1. Further investigation of this correlation showed a nonlinear relationship between the breeding values for PCL1 and PLA$_a$ but a strongly linear relationship between DOV1 and PLA$_a$ (Figure 1). Therefore, in the current population, selection against sires with low breeding values for PLA$_a$ would also select against sires with high breeding values for DOV1 but at the same time not extremely low breeding values for PCL1. Selection for increased PLA could thus be used to decrease profiles with DOV1, but would affect PCL1 unfavorably, albeit to a much lesser extent.

CONCLUSIONS

Measurements of luteal activity within 60 d postpartum with different sampling intervals had high heritability estimates and strong genetic correlations with the interval from calving to commencement of luteal activity. Progesterone analysis in the monthly milk samples from regular milk recording could be used with high accuracy to select for an earlier start of luteal activity after calving and, at the same time, decrease the frequency of cows with prolonged anovulation postpartum.

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