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# Estimation of Genetic Variation in the Interval from Calving to Postpartum Ovulation of Dairy Cows

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## ABSTRACT

Data on the interval from calving to the commencement of luteal activity of postpartum dairy cows were obtained for 1737 lactations of 1137 British Friesian cows in 11 commercial herds and 1 experimental herd between 1975 and 1982. The interval from calving to commencement of luteal activity was measured using progesterone concentrations of milk samples that were collected three or more times per week from shortly after calving to approximately 100 DIM of the following gestation. Genetic models were fitted using REML and accounting for known genetic relationships. Estimates of heritability and repeatability were 0.28 and 0.28, respectively, for the untransformed data; 0.21 and 0.26, respectively, for log-transformed data; and 0.13 and 0.26, respectively, after reciprocals were considered. In all cases, the heritability was significantly different from 0, and, of three scales, the log transformation had the greater likelihood. The likelihood of the transformation was closely related to the magnitude of the coefficient of skewness, and the power transformation with maximum likelihood was between 0.35 and 0.30, for which heritability was 0.19. The geometric mean interval was 25.6 d; coefficient of variation was 37%; and herds, years, parity, and season all had significant effects upon the interval to commencement of luteal activity. The postpartum interval grew longer by 2.2% with each parity [confidence interval 95% (1.1%, 3.0%)] and showed seasonal variation. Cows calving during spring took 1.21 times longer to commencement of luteal activity than did cows calving during autumn [95% confidence interval (1.13, 1.29)]. Genetic regression on PTA of the sire for milk, fat, and protein yields and for fat and protein percentages and on a national economic index were carried out using a subset of animals during 721 lactations. The regression was positive for fat percentage, but not significantly different from 0 for others. The magnitude of the heritability estimate

in this study indicates that the postpartum interval to commencement of luteal activity may be useful for selecting cattle for improved fertility because shorter intervals have been postulated to be correlated with higher reproductive efficiency.

(**Key words:** heritability, postpartum ovulation, luteal activity)

**Abbreviation key:** CLA = commencement of luteal activity,  $h^2$  = heritability,  $P_4$  = progesterone, PP = postpartum,  $r^2$  = repeatability.

## INTRODUCTION

Low fertility affects the profitability of the dairy enterprise (1, 4, 7, 20) and the rate of genetic progress for selected traits (6, 22). Nevertheless, most current breeding programs use indices that weight yield and type traits more than fertility traits. This practice has resulted in substantial genetic progress for yield, but is likely to cause reduced fertility given the reported negative genetic correlation between fertility and yield (12, 19, 23).

The relative weights in genetic selection indices depend not only on the economic value of the phenotype but also on the ability to discriminate among genotypes of different merit. The low heritability ( $h^2 \leq 0.09$ ) for traditional fertility parameters, such as days open (17), calving interval (5), days to first service (14), and services per conception (14), makes discrimination of more fertile genotypes difficult and has consequently frustrated selection for fertility. The interval to first service, days open, calving interval, and number of services per conception are to a large extent influenced by the herd management policy, although the number of services per conception has been argued (18) to be more inherently associated with physiological functions. Therefore, these traits are a poor reflection of the inherent capacity of the cow to establish ovarian function postpartum (PP), to show overt estrus, or to conceive and maintain pregnancy when inseminated at the appropriate time. In an attempt to identify heritable parameters that were associated with fertility, this study measured the amount of genetic variation in the interval be-

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tween calving and the establishment of ovarian activity of dairy cows. This interval is a major component of the biological rhythm of the dairy cow and has been found to be favorably correlated with the more usual measures of fertility (A. O. Darwash, G. E. Lamming, and J. A. Woolliams, 1997, unpublished data).

## MATERIALS AND METHODS

### Data

Milk samples with added preservative were collected thrice weekly from British Friesian dairy cows in 20 commercial herds and daily at the University of Nottingham (Sutton Bonington, United Kingdom) experimental farm between June 1975 and March 1982. Samples were taken from shortly after calving until the PP reproductive pattern was established (at least 100 DIM). Parities (lactation number) ranged from 1 to 12 (parities 2 and 4 were the lower and upper quartiles), and 305-d lactation milk yield was  $6490.3 \pm 48.5$  kg (mean  $\pm$  SE;  $n = 904$ ). Calving occurred predominantly between September and February (77.5%). During each lactation, calving difficulty, uterine infection, general reproductive problems, treatment with medicinal preparations for reproductive disorders, and insemination data were recorded. Data on pedigree and calving dates were obtained from the respective farms and from the national milk recording scheme of the Milk Marketing Board of England and Wales. Information on the PTA of bulls was obtained from the results of national evaluations computed by the Animal Data Centre of the United Kingdom.

### Progesterone Radioimmunoassay

Milk progesterone ( $P_4$ ) concentrations were measured within 1 wk of collection in unextracted aliquots of whole milk using radioimmunoassay (3, 15). The antiserum was BF465 number 6 (9). The intraassay and interassay coefficients of variation were 8.9 and 10.3%, respectively. The limit of sensitivity, defined as twice the standard deviation of the control values, was 0.38 ng/ml.

### Defining Luteal Activity and Estimating the Interval to PP Ovulation

The PP interval to the commencement of luteal activity (CLA) was determined from  $P_4$  profiles of milk. For herds sampled three times per week, two consecutive readings of  $P_4 > 3$  ng/ml indicated the

occurrence of luteal activity, but, for the university herd, four consecutive readings were required to indicate the occurrence of luteal activity. The PP day of the first of these elevated readings defined the interval to CLA. On average,  $P_4$  concentrations  $> 3$  ng/ml were detected 4 to 5 d ( $\bar{X} = 4.5$  d) after estrus (3), and, on average, the interval to CLA would overestimate the crossing of this threshold by 1.16 d (derived from the protocol of thrice weekly sampling); thus, the estimated interval to PP ovulation was equal to the measured interval to CLA minus 5.7 d.

### PTA

When possible, PTA were obtained for the bulls used. Available traits were yields of milk, fat, and protein; percentages of fat and protein; and a profit index based upon yield traits that reflects economic value in the United Kingdom (27). For the 111 sires with an available PTA, the minimum, lower quartile, and median reliabilities were 0.56, 0.85, and 0.95, respectively. All PTA were defined with respect to the 1995 genetic base in the United Kingdom (i.e., denoted PTA95 in the United Kingdom).

### Statistical Analysis

A total of 2349 lactation records had CLA recorded (Table 1). Lactation records that included retained placenta, hormonal treatments, or uterine infections occurring prior to CLA were removed, reducing the number of lactations to 2165. Information on yield and lactation length was not recorded on many of the smaller farms, reducing the number of lactations to 1737 (73.9%) of the original records from 1137 cows in 12 herds, forming 147 paternal-half sib groups (the largest was 44) and 1103 maternal half-sib groups (including single groups with the largest maternal half-sib group size of 3). Records of cows with unknown pedigree were included, and parents were assumed to be unique individuals and to each have only a single offspring. Calving dates were grouped into four seasons of three months each: winter, spring, summer, and autumn commenced in December, March, June, and September, respectively. The data were analyzed with REML (11) using ASREML software (A. R. Gilmour, R. Thompson, B. R. Cullis, and S. Welham, 1996, *ASREML User's Manual*, unpublished). Fixed effects included in the model were parity, season, year, and herd. The random model estimated the additive genetic variance ( $\sigma_a^2$ ) utilizing the known pedigree and permanent environmental variance ( $\sigma_c^2$ ) utilizing the repeated records on cows

over several lactations. Investigation of additional random effects of the two- and three-way interactions of herd, year, and season (116 classes) showed these to increase the log likelihood collectively by <0.1; therefore, only a single random effect that accounted for this three-way interaction was included in the final model. Thus the linear model was

$$Y_{ijklmn} = \mu + \alpha_i + \beta_j + \gamma_k + \delta_l + \gamma_{ikl} \\ + \pi_m + \phi_m + \epsilon_{ijklmn}$$

for cow  $m$  in herd  $i$  ( $i = 1, \dots, 12$ ) and parity  $j$  ( $j = 1, \dots, 12$ ), calving during year  $k$  ( $k = 75, \dots, 82$ ) during season  $l$  ( $l = 1, \dots, 4$ ) with breeding value  $\pi_m$  and permanent environment effect  $\phi_m$ . The  $\pi_m$  were assumed to have a multivariate normal distribution with a mean of 0 and (co)variance  $\sigma_a^2 \mathbf{A}$ , where  $\mathbf{A}$  is the numerator relationship matrix of the cows derived from the relationships available in the data;  $\gamma_{ikl}$ ,  $\phi_m$ , and  $\epsilon_{ijklmn}$  were assumed to be independent and normal random variables, all with a mean of 0 and with variances  $\nu^2$ ,  $\sigma_c^2$ ,  $\sigma_e^2$ , respectively. Functions of the variance components that were of special interest were the phenotypic variance  $\sigma_p^2 = \sigma_a^2 + \sigma_c^2 + \sigma_e^2$ , the  $h^2 = \sigma_a^2/\sigma_p^2$ , and the repeatability ( $\mathbf{r}^2$ ) =  $(\sigma_a^2 + \sigma_c^2)/\sigma_p^2$ . Confidence intervals for  $h^2$  were constructed from the likelihood profile by finding the interval for which the  $\log_e$  likelihood was within  $x/2$  of its maximum, where  $x$  was the appropriate percentage point of the chi-square distribution with 1 df.

Transformations of the interval from calving to CLA were investigated using the family of power transformations (2). These methods consider the family of power transformations indexed by  $\lambda$ ,  $(\text{CLA})^\lambda$ , which included as special cases an additive model fitted to CLA itself ( $\lambda = 1$ ), an additive model fitted to the reciprocal of CLA ( $\lambda = -1$ ) that can be viewed as a rate of return to luteal activity, and an additive model fitted to the logarithm of CLA ( $\lambda = 0$ ) that is equivalent to fitting a multiplicative model to CLA itself. The general form of the family for a dependent variable  $y$  is given by  $y_\lambda = (y^\lambda - 1)\dot{y}^{1-\lambda}\lambda^{-1}$  where  $\dot{y}$  is the geometric mean of  $y$ . When  $\lambda = 0$ , the dependent variable was the natural logarithm divided by the geometric mean. The linear model just described was fitted to CLA for nine values of  $\lambda$  in the range of  $-1$  to  $1$  inclusive, and the likelihood was considered as described by Gianola et al. (10); based on these results, further values of  $\lambda$  were used to narrow the location of the optimum value. The choice to present the more detailed results of the analyses was made between the three special cases because of their more

immediate interpretation in relation to the observed trait. The coefficient of skewness, defined as the third moment about the mean standardized by the cube of the standard deviation, was calculated for each transformed variable.

Hypothesis tests for any nonzero effect of the fixed factors were Wald tests based on the weighted sums of squares of the fixed effects and the inverse of the average information matrix. For the effects of year and herd, only these tests were conducted. For the effect of season, the six paired comparisons were carried out using separate Wald tests with a Bonferroni correction for size; thus, for each individual comparisons, the probability of Type I error was 0.0085. For parity, the regression coefficient for interval to CLA on parity was calculated from the submodel.

A second analysis of the interval to CLA was made after the data were restricted by including only those lactations from cows with known sires and for which the sires had known PTA. This edit restricted the data to 721 lactations from 485 cows in 7 herds. The cows formed a total of 111 paternal half-sib groups. The PTA for the six yield traits were added, in turn, as a covariate to the linear model described. The PTA for different traits were fitted in turn, and not in a single model, because of high correlations of a genetic origin among PTA. Because, for a small number of sires, the data used in the fitting process represented >10% of the total number of records on which the PTA were based, the data were further reduced by excluding their offspring in order to decrease possible bias from environmental covariation between the dependent variable and the PTA.

## RESULTS

The results describe the untransformed and unadjusted data, followed by the results from the investigation into the appropriate transformation. Results of the analyses using the chosen transformation are also presented.

### Mean Interval to PP Ovulation and CLA

Distributional parameters for the PP interval to CLA for all lactations with information and for those included in further statistical analyses are shown in Table 1. The distribution was also positively skewed (Figure 1). The raw data for further genetic analysis had an arithmetic mean of 26.5 d, a standard deviation of 11.9 d, and a coefficient of variation of 45%. For these data, the average interval to ovulation PP would be estimated as 21.8 d (i.e., 26.5 - 5.7).

TABLE 1. The postpartum interval from calving to commencement of luteal activity (CLA) for all lactations with or without veterinary intervention, retained placenta (RP), or uterine infection (UI) and numbers of lactations with ancillary information.

	Lactations	
	(no.)	— (d) — $\bar{X}$ SD
All records with CLA	2349	28.7 14.6
Without intervention, RP, or UI	2165	27.3 12.0
With full data on fixed effects	1737	26.5 11.9
With sire PTA information	721	25.9 11.1

**Transformations for the Interval from Calving to CLA**

Table 2 shows the likelihood profile obtained from fitting the model to different power transformations applied to the interval from calving to CLA. The  $r^2$  was relatively constant over the range of potential transformations considered, but the  $h^2$  was sensitive to the transformation, decreasing from 0.280 ( $\lambda = 1.0$ ) to 0.133 ( $\lambda = -1.0$ ). The optimum transformation was between  $\lambda = -0.35$  and  $-0.30$ , for which  $\log_e$  likelihood was  $-4797$ , estimates of  $h^2 = 0.187$ , and  $r^2 = 0.266$ . The likelihood ratio test for a null hypothesis of  $h^2 = 0$  was significant ( $P < 0.05$ ) when  $\lambda = -1.0$ , and the significance of the test increased as  $\lambda$  increased. Table 2 shows that the likelihood of the

transformation varied closely with the magnitude of the coefficient of skewness. Because the logarithmic transformation ( $\lambda = 0$ ) had a greater likelihood than either the reciprocal or identity transformations, the remaining analyses were conducted using  $\log_e$  (CLA), although all three were outside the 95% confidence interval for the optimum transformation.

For  $\log_e$  (CLA), the estimates were  $h^2 = 0.214$  with the 95% confidence interval (0.05, 0.33) and  $r^2 = 0.265$  with the 95% confidence interval (0.19, 0.34). The likelihood ratio test for  $h^2 = 0$  was significant ( $P < 0.01$ ). From this analysis, the estimated geometric mean interval from calving to CLA was 25.55 d, and the coefficient of variation was 37%, calculated from  $100[\exp(\sigma_p^2) - 1]^{0.5}$  where  $\sigma_p^2$  was the phenotypic variance on the logarithmic scale.

**Effect of Parity**

The effect of parity is shown in Figure 2. The interval from calving to CLA became progressively longer as number of parity increased. The regression submodel estimated an increase in the interval of 2.2% per parity ( $P < 0.001$ ) with a 95% confidence interval of (1.1%, 3.0%). From the regression, over a productive lifetime of 6 lactations, the PP interval from calving to CLA would be predicted to increase by 11.5%.

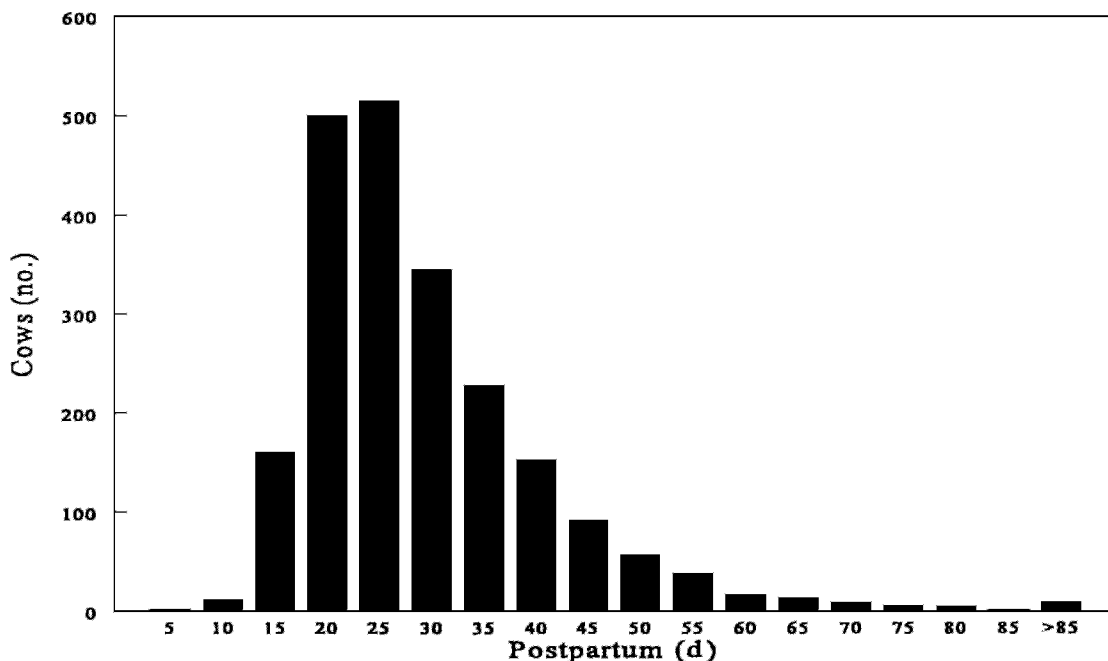


Figure 1. The frequency distribution of the postpartum interval to commencement of luteal activity of dairy cows derived from 2165 lactations with no retained placenta, uterine infections, or veterinary intervention prior to commencement of luteal activity.

TABLE 2. The effect of the power transformations ( $\lambda$ ) on estimates of heritability ( $h^2$ ) of the postpartum interval to commencement of luteal activity, proportion of variance because of variance in permanent environment ( $c^2 = \sigma_c^2/\sigma_p^2$ ), repeatability ( $r^2 = h^2 + c^2$ ),  $\log_e$  likelihood ( $\log_e L$ ), and the coefficient of skewness.

$\lambda$	Parameter estimates			$\log_e L$	Skewness
	$h^2$	$c^2$	$r^2$		
-1.0 (reciprocal)	0.133	0.125	0.258	-4900	-1.19
-0.7	0.157	0.105	0.262	-4828	-0.57
-0.4	0.181	0.084	0.265	-4798	-0.12
-0.1	0.205	0.060	0.266	-4808	0.28
0 (logarithm)	0.214	0.052	0.265	-4820	0.41
0.1	0.222	0.042	0.264	-4836	0.54
0.4	0.249	0.009	0.258	-4911	0.95
0.7	0.267	0.000	0.267	-5029	1.43
1.0 (observed)	0.280	0.000	0.280	-5191	2.00

### Effect of Season

The geometric means for the interval to CLA of primiparous cows during the four calving seasons were 25.5, 27.9, 25.1, and 23.1 d for winter, spring, summer, and autumn, respectively. The overall test for seasonal effects was significant ( $P < 0.001$ ), and specific contrasts showed that the interval during autumn was shorter than during any other season; the interval during winter and summer was shorter than during spring. Cows calving during spring took 1.2 times longer PP to CLA than did cows calving during autumn [95% confidence interval(1.13, 1.29)].

### Effects of Herd and Year

Variation among the herds represented was significant ( $P < 0.01$ ); the geometric mean of the interval to

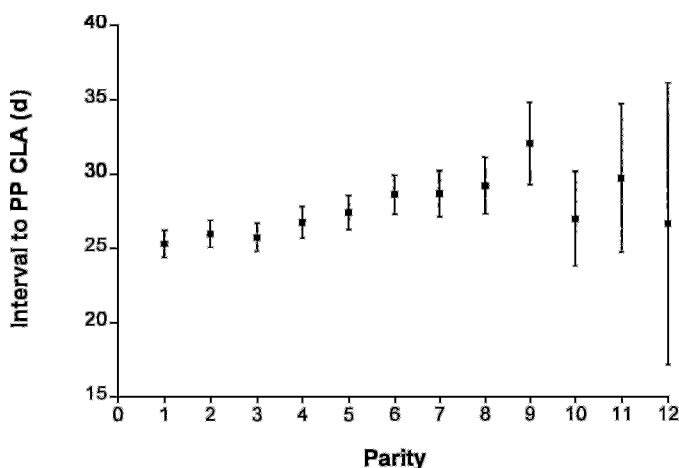


Figure 2. The effect of parity (lactation number) on the postpartum (PP) interval to commencement of luteal activity (CLA). Data are expressed as means and standard errors.

CLA in individual herds ranged from 24.1 to 33.6 d. Annual variation was also present ( $P < 0.001$ ), and the geometric mean PP interval to CLA ranged from 23.1 d during 1977 to 31.5 d during 1979.

### Genetic Regression of $\log_e$ (CLA) on Measures of Yield

Genetic regressions of  $\log_e$  (CLA) on PTA were  $-0.00033$  (SE = 0.00017) for milk yield, 0.0014 (SE = 0.0042) for fat yield,  $-0.0086$  (SE = 0.0055) for protein yield, 0.745 (SE = 0.277) for fat percentage, 0.189 (SE = 0.496) for protein percentage, and  $-0.0016$  (SE = 0.0014) for United Kingdom profit index. The only coefficient that was significantly different from 0 was the positive regression for fat percentage ( $P < 0.01$ ), but the negative regression for milk yield approached significance ( $P < 0.1$ ). The magnitude of the regression on PTA for fat percentage was such that daughters of a bull with EBV of one genetic standard deviation (approximately 0.31% in United Kingdom) above the mean would take 1.26 times as long to establish ovarian activity as would daughters of bulls with one genetic standard deviation below the mean (i.e., approximately 6.5 d longer). Genetic variation in the interval to CLA remained significantly greater than 0 after regression on the EBV. Restricting the regression to bulls with >90% of their daughters coming from outside the data produced no qualitative change to the regression.

### DISCUSSION

This study has provided the first clear evidence that a substantial proportion of the variation among individuals within a dairy breed during the period taken to reestablish PP ovarian activity was additive

genetically. Second, this study, conducted largely on commercial farms, has shown that the PP interval to CLA grew longer as parity increased and that trends were seasonal; the peak occurred during spring, and the trough occurred during autumn. Variation among herds and years was also identified. The estimated  $h^2$  of 0.21 on a logarithmic scale suggests that the magnitude of  $h^2$  might be sufficient to be of practical value for selection programs.

Few previous studies (8, 13, 28) examined genetic variation in the resumption of ovarian activity of PP dairy cows, but no previous work has quantified the extent of the genetic variation within a breed. Those studies, in contrast to the present work, measured only the extent of variation in the PP interval to estrus and ovulation associated with genetic differences in yield. In such studies, the expected difference depended on the genetic correlation of the measured traits with yield, and, if the correlation was 0, the expected difference was 0. In only one of those studies was evidence of genetic variation found (28). No significant difference was observed between Holstein and Jersey breeds in the interval to PP ovulation (8).

The major limitation for examining genetic variation in reproductive parameters, such as interval to first PP ovulation, has been measurement of sufficient numbers of cows in an appropriate design, using noninvasive techniques, in order to quantify the additive genetic variance. The use of routine  $P_4$  measurement has provided a practical means of achieving this result. Previous studies have used either rectal palpation alone (28) or palpation in conjunction with thrice weekly blood sampling for  $P_4$  determinations (8, 13).

The data collected in this study were too few to provide credible estimates of the genetic correlations with other aspects of performance such as yield. However, from a subset of the data, the possible genetic relationships with yield were explored by regressing the PP interval to CLA on the PTA for yield traits. The regression coefficient on milk yield was negative, and, although only approaching significance ( $P < 0.1$ ), this result is in agreement with the phenotypic relationship observed for Jersey cows in which those cows yielding more milk ovulated sooner than lower yielding herdmates (8), but is in disagreement with results of a line with high genetic merit for milk yield that took 2 d longer to reestablish ovarian activity (28). Others (13) found no significant difference between Friesian cows of high (10,814 kg) and low (6912 kg) genetic merit for milk yield in the interval to PP ovulation. In contrast to the negative association between milk yield and CLA, the

relationship was positive ( $P < 0.01$ ) between the interval to CLA and milk fat percentage. Other regressions were not significantly different from 0, and the imprecision of these estimates demonstrated the need for care in interpretation.

As with any estimate of  $h^2$ , biases existed because of genetic selection either directly from selection within herds on reproductive performance, some of this through natural selection, or indirectly via selection on correlated traits (potentially yield or type). Assuming an additive model of infinitesimal alleles, the effect of such directional selection was to underestimate the true  $h^2$ , and the extent of the bias depended upon the intensity of the selection pressure and the accuracy of the selection on the interval to CLA. Genetic selection on reproductive parameters occurs mainly through culling decisions made by farmers based on traditional traits such as days open, and, therefore, both the intensity of selection and the accuracy of selection (given the low  $h^2$  of days open) are likely to be small. The magnitude of indirect selection through genetic relationships with yield are difficult to determine, and the existing evidence for such selection is contradictory [this study; (8, 13, 28)]. Another source of bias is the incomplete pedigree information for the sires and dams, which is also expected to lead to underestimation of  $h^2$  (24).

We consider the first source to be unlikely because, for a great majority of cows, the measurement of the PP interval to CLA occurs within the first 6 wk of lactation, and, during this period, commercial decisions on voluntary culling or rebreeding are unlikely to be implemented. There is *prima facie* evidence in Table 1 for weak selection of records for analysis favoring shorter intervals. In conclusion, we think that selection would have introduced only a small bias and would have resulted in an underestimate of  $h^2$ .

The sensitivity of the  $h^2$  estimate to the transformations applied may indicate nonlinearity of the regression of the EBV on the phenotype. The transformations would be considered to have weighted the phenotypic distribution differentially so that relatively more weight was given to the shorter intervals to CLA as the power transformation moved from the identity to the reciprocal. The emphasis on the shorter intervals was associated with the smaller estimates of  $h^2$ , which might imply that the opportunities for reducing the incidence of long intervals might be greater than those for increasing the short intervals. Such reasoning would also reinforce the conclusion that any inadvertent data selection carried out for inclusion in the analysis (see Table 1) would have led to underestimates of  $h^2$ .

The estimate of  $h^2$  obtained in this study for the PP interval to CLA can be contrasted with the very low estimates obtained for traditional measures of fertility, such as interval to first service, days open, or number of services per conception (5, 12, 14, 19, 26). Many of these latter measures might be profoundly affected by management decisions that, in turn, may be influenced by yield, making interpretation of such data complex. Phenotypically, the PP interval to CLA has been associated with traditional measures of fertility under experimental conditions, and shorter intervals have been shown to reduce the number of days open and to increase the chance of successful first insemination when conducted after a given time PP (28). Furthermore, the chances of success at a given insemination have varied with the number of cycles after their reestablishment PP (25, 28).

The results of this study suggest that a better approach to the genetic improvement of fertility might be to replace the traditional measures, defined by concerns of the farmer, with a more biological approach that considers a given number of days PP to CLA plus a specific number of normal cycles. This approach would focus future genetic studies on fertility of dairy cows on 1) refining the estimate of genetic variation in the interval to CLA and measuring its covariances with other traits of economic interest (principally yield) and 2) determining the extent of genetic variation and covariation associated with conception at a given number of cycles PP. The refinements in the  $h^2$  estimate need to include measurement of the interval from calving to CLA on a larger sample of cows from a more modern dairy breed with current management practices. The results of such a study (inevitably long-term, but now in progress) should enable better assessment of the commercial application for intended calving intervals and yield as the genetic merit for the latter advances.

If the magnitude of the current estimate of  $h^2$  for the interval to CLA is confirmed and the genetic relationships with fertility are similar to those already described for phenotypes, then the use of this interval in an index with other traits describing the selection goal is a tractable proposition. The magnitude of the  $h^2$  is sufficient to suppose that the index weight, which would also depend on the economic weight attached to fertility measures and the genetic covariances with yield in the production system, would make the trait worth measuring, particularly for daughters of bulls undergoing progeny testing. The routine collection of milk samples for  $P_4$  assay is certainly feasible, as it is for fat and protein content. As a result of such an index, the producers could make more informed selection decisions.

The variation among cows in the resumption of PP luteal activity that was found in this study may be due to inherited differences in the sensitivity to GnRH signaling of the pituitary and ovary. Therefore, the  $h^2$  of the response to GnRH challenge of heifers and cows and its association with PP resumption of ovarian activity deserves investigation. The response of beef bulls to GnRH was highly heritable (16). The effect of season on the return to PP ovulation is dependent on the geographical location of the herd and on feeding and management practices. The lowest interval to CLA during autumn (23.1 d) that was found in this study was comparable with results of Fonesca et al. (8), who found that cows calving during September to November had intervals to PP ovulation that were 6.5 d shorter than those of cows calving during December to February. In the present study, the longest interval (27.9 d) was for cows calving during the spring, confirming an earlier report on a subset of the data (3). This result may be due to the effects of pasture feeding on the energy balance in the cow or the effects of the ratio of light to dark periods or ambient temperature on the hypothalamic-pituitary-ovarian axis.

The effect of parity (Figure 2)—that younger cows had earlier first PP ovulation than did older cows—was in agreement with the findings of Fonesca et al. (8).

## CONCLUSIONS

The interval to the CLA PP within a population of Friesian cows in the United Kingdom using  $P_4$  determinations was heritable ( $h^2 = 0.21$ ;  $P < 0.01$ ) and repeatable ( $r^2 = 0.26$ ;  $P < 0.001$ ). The optimum power transformation appeared to be between  $-0.35$  and  $-0.30$ , and the logarithmic transformation fitted better than either the identity or reciprocal transformation. The interval grew longer with each subsequent parity and showed seasonal variation (a peak during spring and a trough during autumn). The  $h^2$  estimate indicates that selection for shorter intervals to CLA may be feasible. However, further studies are needed to measure the genetic and environmental associations of the PP interval to CLA with yield and to define more closely the relationship of the interval with more traditional measures of fertility so that selection indices can be developed using appropriate economic weights.

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