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Theriogenology

Theriogenology 63 (2005) 950–971

www.journals.elsevierhealth.com/periodicals/the

The effect of strain of Holstein-Friesian cow and feeding system on postpartum ovarian function, animal production and conception rate to first service

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Received 18 January 2004; received in revised form 26 May 2004; accepted 29 May 2004

Abstract

Three strains of Holstein-Friesian (HF): high production North American (HP), high durability North American (HD) and New Zealand (NZ) cows were assigned, within strain, to one of three pasture-based feeding systems: (1) the Moorepark (control) system (MP), (2) a high concentrate system (HC), (3) a high stocking rate system (HS). Ovarian function was assessed using milk progesterone samples, collected from 117 cows in each of two successive years, with 81 animals being common to both years. Milk samples were collected thrice weekly, beginning day 5 post-calving and continued to day 26 after first AI. Data from animals subsequent to reproductive hormonal treatment were removed from the analysis. Feed system and strain of HF by feeding system interaction had no significant effect on re-establishment of ovarian activity and subsequent conception rate to first AI. Strain of HF had no significant effect on interval to commencement of luteal activity (CLA). The mean interval to CLA was 32.9 days (S.E. 1.18), ranged from 6 to 100 days, with 42 and 85% of cows ovulating by day 26 and 60, respectively. The HD (62%) and NZ (57%) strains had a higher conception rate to first AI than the HP strain (40%), ($P < 0.05$). Retrospective analysis categorised all cows into four quartiles based on interval to CLA (<20 days, 20–26 days, 27–44 days and >44 days). Cows in the first and fourth CLA quartiles had a longer calving to conception interval ($P < 0.05$). Cows with abnormal progesterone profiles (38.4%) had an earlier mean calving date, with a similar submission rate and conception rate to first service compared to cows with normal hormonal profiles. There was no significant difference in luteal activity or reproduction performance, apart from calving to conception interval, between cows that conceived or did not conceive to first service. These

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doi:10.1016/j.theriogenology.2004.05.014

results indicate that while conception rate to first service differed between strains of HF cow, this was not associated with differences in the onset and pattern of luteal activity post partum.

Keywords: Strain; Cow; Feed system; Ovarian function; Milk progesterone; Conception rate

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1. Introduction

Milk production in Ireland is primarily pasture-based and involves seasonal calving [1]. In a typical seasonal herd in Ireland, breeding starts on a fixed calendar date in spring, between late April and early May. The key breeding objective is to achieve the highest pregnancy rate in the shortest period of time after the start of the breeding season in order to achieve a concentrated calving pattern during the following season [2]. This is also required to maintain a calving interval of around 365 days. In recent years, however, Irish dairy cow fertility has declined [3,4]. Considerable importance has been placed on interval to first ovulation as a measure of reproductive efficiency because cows must be cyclic before the breeding season. Early commencement of luteal activity (CLA) post partum has been linked to improved reproductive performance in many studies [5–7].

Up to the mid-1980s the predominant breed of dairy cow in Ireland was the British Friesian. Over the last 15 years there has been significant introduction of North American Holstein-Friesian (NAHF) genetics into the Irish dairy cow population, increasing from 9% in 1990 to 65% in 2001 [4]. During this period, annual milk yield per cow has increased from approximately 5000 to 6000 kg. In Ireland, genetic parameters predict an antagonistic genetic relationship between milk yield and reproductive traits [8,9]. These values are supported by the results from controlled experiments comparing genetic groups across feeding systems [10,11] and retrospective surveys [12]. In other countries aggressive genetic improvement within the NAHF for increased milk yield has resulted in similar negative effects on cow fertility [13,14].

It has been reported that the interval to first ovulation in the modern Holstein-Friesian cow is longer and the prevalence of anoestrus is greater at the start of the breeding season [15]. Most investigations would suggest that the reason for the delay in interval to first ovulation is greater negative energy balance (NEB). NEB reduces postpartum LH pulsatility and, therefore delays the resumption of ovarian activity [16]. Commencement of cyclicity post partum has been linked to such factors as: nutrition, body condition, milk production, breed, age, month of calving and disease status [17–21]. The New Zealand Holstein-Friesian cow has been selected for increased fat and protein yield in a given volume of milk, longevity and fertility (including a cost for maintenance) under seasonal intensive pastoral dairy farming [22]. In contrast, North American Holstein-Friesian cows have been selected for increased milk production and protein yield, under intensive concentrate feeding systems, where a 365-day calving interval is not as important a factor because calving is year round.

Measures such as interval between calving and the commencement of luteal activity determined by milk progesterone profiles have been suggested as suitable selection criteria for fertility [23–25]. Heritability estimates for these variables (0.16–0.28) are generally higher than measures calculated using service data [23,25,26]. The higher heritability estimates are observed because the genetic variance is more effectively quantified, as CLA is free of management influences such as oestrous detection or decisions delaying insemination.

The objectives of the current study were to determine the influence of strain of Holstein-Friesian cow and pasture-based feeding system on re-establishment of ovarian activity post partum and subsequent conception rate to first service.

2. Materials and methods

This study was carried out at Curtins farm, Moorepark Research Centre from January 2002 to June 2003. It formed part a 5-year study designed to examine the biological and economic performance of three strains of HF cows on three different pasture-based feeding systems. In each year 117 animals were studied. The dataset included 39 animals of each strain divided into three feed system groups, to leave nine groups of 13 animals. In year 1, there were eight animals of second parity and five primiparous animals in each group while in year 2, there were seven, five and one animals of third, second and first parity, respectively, in each group.

2.1. Animals

Three strains of HF cows were compared: high production North American (HP), high durability North American (HD) and New Zealand (NZ). The top 50% of cows in the Moorepark herd (based on pedigree index for milk production) were inseminated with semen from five North American sires to generate the HP strain. The five sires were chosen on the basis of their superior pedigree index for milk production. The mean predicted differences (PDs) for the five sires were +306 (S.D. 56.2) kg milk, 11.9 (S.D. 2.77) kg fat, 12.8 (S.D. 2.59) kg protein, 0.00 (S.D. 0.069) g fat/kg, 0.05 (S.D. 0.043) g protein/kg, −0.88 (S.D. 1.10) % survival and +1.08 (S.D. 2.46) days calving interval. The average proportion of HF genes in the HP strain was 90%. Based on pedigree index for milk production, the bottom 50% of cows in the Moorepark herd were inseminated with semen from five North American sires to generate the HD strain. The five sires were chosen on the basis of their superior milk production, fertility and linear (muscularity) traits. The PDs for the five sires were +110 (S.D. 128.3) kg milk, 9.3 (S.D. 4.9) kg fat, 8.1 (S.D. 2.2) kg protein, 0.10 (S.D. 0.13) g fat/kg, 0.09 (S.D. 0.07) g protein/kg, −0.08 (S.D. 1.16)% survival and −1.5 (S.D. 1.87) days calving interval. The average proportion of HF genes in the HD strain was 80%. The top 50% and bottom 50% of cows in the Moorepark herd (based on pedigree index for milk production) were used to generate the HP and HD strains respectively, in order to develop differences in milk yield potential between them. The NZ strain animals were imported as embryos from New Zealand and implanted into 13-month-old HF-heifers in Moorepark Research Centre. They were selected using the highest possible genetic merit expressed in the New Zealand genetic evaluation system (Breeding Worth). On average, 87.5% of the NZ strain genes were of New Zealand HF ancestry. Jersey genes contributed up to a maximum of 12.5%, with the remaining genes of North

American HF ancestry. The mean PDs for the five sires were +65 (S.D. 9.2) kg milk, 13.4 (S.D. 4.6) kg fat, 6.1 (S.D. 1.0) kg protein, 0.21 (S.D. 0.089) g fat/kg, 0.08 (S.D. 0.017) g protein/kg, +1.22 (S.D. 1.09) % survival and −2.1 (S.D. 0.82) days calving interval. The PDs of the sires were obtained from the November 2003 international evaluations of the Animal Centre, Uppsala, Sweden using the technique known as multi-trait across-country evaluation (MACE).

2.2. Feeding systems

The three feeding systems compared were: the Moorepark system, with high milk output from pasture (MP), a high concentrate feeding system (HC) and a high stocking rate feeding system (HS). The MP system had an overall stocking rate of 2.47 cows/ha, a nitrogen (N) fertiliser input of 300 kg N/ha (from early-January to late-September) and a planned concentrate input of 350 kg/cow over the total lactation in both years. The HC had a similar overall stocking rate and N input as the MP system but a planned concentrate input of 1500 kg/cow. The HS had similar concentrate and N inputs as the MP system but it had a higher overall stocking rate of 2.74 cows/ha. The aim of this treatment was to graze to a lower post-grazing sward surface height. The MP and HC feeding systems were designed to allow each strain to express its potential largely unrestricted by limitations in feed supply. In each year, animals were turned out to pasture by day from 1 February and by day and night from 10 March. The animals were maintained on grass by day and night until 1 November in both years when they were housed by night and continued on pasture by day for a further 3 weeks. While housed, all animals received grass silage ad libitum (700 g/kg DM digestibility).

All primiparous animals were on a similar feeding system for the first 4 weeks of lactation receiving 7 kg of concentrates daily in two equal meals. Animals were blocked within strain into groups of three, on the basis of calving date, milk production over the first 4 week of lactation, live-weight and condition score and then randomly assigned to one of three feed systems. Once allocated to a feed system, animals were retained on the same feed system in the subsequent lactation. The feed systems were applied immediately post partum to all pluriparous animals. The ingredient composition of the concentrate feed (kg/t as fed) was as follows: barley 250, corn gluten 260, beet pulp 350, soya-bean meal 110, and minerals plus vitamins 30. The chemical composition of the concentrate offered (g/kg DM) was 180 and 800 crude protein and cellulase gammanase digestibility, respectively. The concentrates were offered individually to the cows in the milking parlour. Half of the daily allowance of concentrate was offered at each milking (AM and PM). The concentrate supplementation pattern for each feed system is displayed in Table 1.

2.3. Reproductive management

Immediately post-calving, cows were visually observed three times daily for signs of oestrus. Tail paint was used as an aid to oestrus detection. All pre-breeding oestrous events were recorded. Cows were visually observed four times daily for signs of oestrus during the breeding season, which commenced on 20 April in each year and finished 13 weeks later on 20 July. Only semen from sires with good sperm motility and high percentage of live sperm

Table 1
Concentrate supplementation strategy[a] (kg/cow/day)

Feed system	Calving to 15 March	15 March to 31 March	1 April to early May	Early May to end of lactation
Moorepark	6	4	2	0
High stocking rate	6	4	2	0
High concentrate	8	8	6	4

[a] All primiparous animals were maintained on 7 kg/day for a pre-experimental period of 4 weeks post calving.

was used in AI. Approximately 35–42 days post partum each cow was examined to assess the degree of uterine involution and the presence of a corpus luteum using trans-rectal ultrasound imaging (ALOKA SSD 500 V with a 5 MHz transducer, ALOKA Ltd., Tokyo, Japan). Cows with endometritis, pyometra, anovulatory measures or ovarian cysts were treated appropriately using combinations of gonadotrophin releasing hormone analogue, progesterone, oestradiol, prostaglandin and uterine infusions (antiseptic or antimicrobial) in 8–10-day treatment programmes, as necessary. Cows were inseminated, using AI, by the same professional inseminator each year, after morning milking. Pregnancy examinations were performed by trans-rectal ultrasound imaging at 30–37 days and 60–67 days after AI, and also by palpation per rectum at 6 weeks after the end of the breeding season.

2.4. Measurements

Milk yield was recorded on 5 consecutive days per week. Animals were milked twice daily, at 07.00 and again at 15.30. Milk fat, protein and lactose concentrations were determined using a Milkoscan 203 (Foss Electric DK-3400, Hillerod, Denmark), from successive morning and evening samples collected once weekly. Cow liveweight was recorded once weekly after morning milking. Each liveweight was recorded electronically, using portable weighing scales and Winweigh software package (Tru-Test Limited, 241 Ti Rakau Drive, Aukland, New Zealand). The scales were calibrated weekly against known weights. Body condition score (BCS) was recorded every 3 weeks during the lactation on a 1–5 scale (1 = emaciated, 5 = extremely fat) with increments of 0.25 [27]. The first liveweight and BCS data were recorded 24-h post partum. To avoid stressing animals during the data collection process, all liveweight and BCS measurements were taken by experienced staff familiar to the animals.

2.5. Milk sampling and progesterone analysis

Milk samples, representative of the whole milking, were collected thrice-weekly on Mondays, Wednesdays and Fridays during morning milking. Sampling began 5 days post partum and continued until 26 days after first AI. Immediately post milking, one potassium dichromate preservative tablet (Lactab Mark III, Thompson & Capper Ltd., Cheshire, England) was added to each sample and was subsequently stored at 4 °C until analysis. Milk progesterone concentrations were measured in representative unextracted samples of

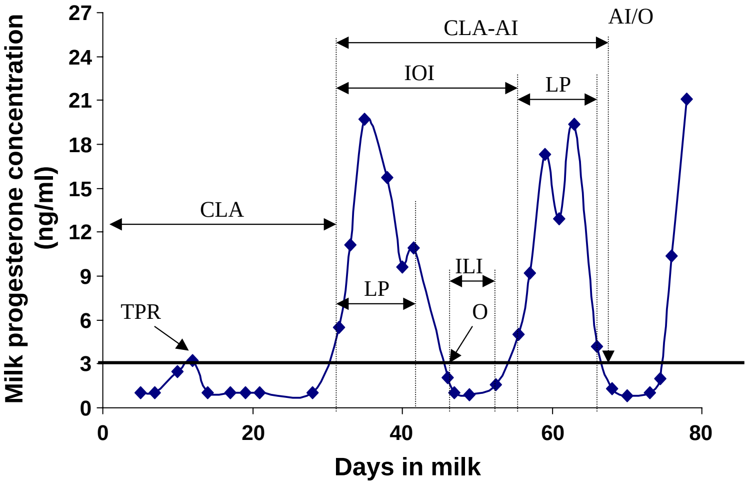

Fig. 1. Reproductive parameters monitored using milk progesterone profiling. Abbreviations: TPR: transient progesterone rise, CLA: commencement of luteal activity, LP: luteal phase, CLA-AI: commencement of luteal activity to AI interval, O: ovulation, IOI: inter-ovulatory interval, ILI: inter-luteal interval.

whole milk using enzymeimmunossay (Ridgeway Science Ltd, Rodmore Mill Farm, Alvington, Gloucestershire, UK) based on the method of [28]. The intra-assay co-efficient of variation for quality control was 15.7% and the inter-assay co-efficient was 13.7%. The sensitivity, calculated using the absorption of the blank standard minus two standard deviations, was 0.5 ng/ml.

2.6. *Defining luteal activity*

Endocrine parameter definitions were calculated based on the work of [29,30]. These parameters are illustrated in Fig. 1. Following calculation some parameters required either addition or subtraction of a sampling bias due to the thrice-weekly sampling protocol. Where required, the correction factor is included in the results. Data for luteal parameters from cows that received hormonal treatments between calving and 26 days after first AI were excluded from the analysis subsequent to treatment, as the consequences of any treatment on progesterone profiles could not be determined. The following reproductive parameters were monitored using milk progesterone profiling from day 5 post partum to day 26 post AI:

2.6.1. *Commencement of luteal activity post partum (CLA)*

As defined by [7,29], a period of luteal activity is defined as the occurrence of two or more consecutive milk progesterone concentrations of ≥3 ng/ml. The period of time from calving to CLA is the number of days from calving to the first day of luteal activity (i.e. the date of the first of two consecutive recordings with ≥3 ng/ml-milk progesterone). When measuring this estimate the sampling routine introduces an overestimate of 1.17 days, on average, which was subtracted from the calculated value.

2.6.2. Luteal phase (LP)

As defined by [29], this is the period of time following ovulation in which a corpus luteum secretes progesterone, measuring ≥ 3 ng/ml in milk. The length of the luteal phase was measured from the time of the first of consecutive milk samples ≥ 3 ng/ml (time T_1) to the final consecutive milk sample of ≥ 3 ng/ml (time T_2). The sampling routine underestimates the interval by, on average, approximately 2.33 days (i.e. $1.17 + 1.17$). Therefore, the corrected interval was reported as $T_2 - T_1 + 2.33$ days. This also means that a luteal phase of less than 4 days cannot be measured. Two or more consecutive samples ≥ 3 ng/ml are required to measure the luteal phase length. Profiles exhibiting single concentrations ≥ 3 ng/ml were classified as transient progesterone rises (TPRs) (see Fig. 1). The timing and frequency of TPRs were recorded as they may, in some instances, have been part of a regular luteal phase, which were not detected by the sampling routine. The number of luteal phases observed from day 5 post partum to day 26 post AI was recorded.

2.6.3. Inter-ovulatory interval (IOI)

This is defined as the period of time from the commencement of one luteal phase to the commencement of the next luteal phase (where the commencement of a luteal phase is defined above). [29] identified this as an objective measure of oestrous cycle length. No inherent sampling bias exists with this parameter.

2.6.4. Interval between commencement of luteal activity and first AI (CLA-AI)

This is the interval from the initiation of the first luteal phase post partum to the day of first service. When measuring this estimate, we corrected for the underestimate of 1.17 days introduced by the sampling routine.

2.6.5. Inter-luteal interval (ILI)

The ILI is defined by [29] as the interval in days between the demise of one corpus luteum and the appearance of the next. This interval is measured from the first milk sample of <3 ng/ml following luteolysis (time T_3) and the last consecutive milk sample <3 ng/ml (time T_4). This measurement introduces a sampling bias of 2.33 days, the same as that for luteal phase length. Consequently, the corrected ILI $= T_4 - T_3 + 2.33$ days.

2.6.6. Atypical ovarian hormone patterns

The four irregular progesterone profiles recorded here were those classified by [29]. Delayed ovulation type I (DOVI) occurs where a milk progesterone concentration of ≥ 3 ng/ml is not achieved for ≥ 45 days post partum. Delayed ovulation type II (DOVII) occurs where the duration of any inter-luteal interval is ≥ 12 days, i.e. 12 days after a luteal phase where no luteal phase begins. Persistent corpus luteum type I (PCLI) occurs where milk progesterone concentrations of ≥ 3 ng/ml are observed for ≥ 19 days during the first luteal phase post partum. Persistent corpus luteum type II (PCLII) occurs where milk progesterone concentrations of ≥ 3 ng/ml are observed for ≥ 19 days during the second and subsequent oestrous cycles post partum.

2.6.7. Embryonic mortality

Two types have been classified: fertilization failure/early embryo mortality (FF/EEM) and late embryo mortality (LEM). It is impossible to distinguish between fertilization failure and EEM, using milk progesterone profiles. This group are defined by [31] with the following criteria:

Day 0–2_ milk progesterone concentration of <3 ng/ml and
Day 5–7_ milk progesterone concentration of $\geq$3 ng/ml and
Day 20–24_ milk progesterone concentration of <5 ng/ml or the cow was re-inseminated before day 20–24, or was not pregnant after ultrasound pregnancy examination at day 30–37.

The second type of embryo mortality is late embryo mortality as defined by [29] meeting the following criteria:

Day 0–2_ milk progesterone concentration of <3 ng/ml and
Day 20–24_ milk progesterone concentration of $\geq$8 ng/ml and
Day >24_ milk progesterone concentration of <5 ng/ml or the cow was reserved, or embryo mortality was detected at pregnancy examination.

2.7. Reproductive measurements

A number of fertility performance variables were also calculated; 24 day submission rate (percentage of all cows that calved and were submitted for AI by day 24 of the breeding season), calving to service interval (days from calving to first service), calving to conception interval (days from calving to conception as defined by pregnancy detection at day 30–37 post service without embryo mortality upto 6 weeks after the end of the breeding season), calving to first oestrus (days from calving to first detection of standing oestrus), and conception rate to first service (proportion of the herd confirmed pregnant based on trans-rectal ultrasonography at 30–37 days after first AI that do not suffer embryo mortality up to 6 weeks after the end of the breeding season).

2.8. Data handling

Data handling was carried out using a database programme [32]. A total of nine variables with potential implications for reproductive performance were created from the milk production, liveweight and BCS data. The milk production variables included: milk yield at day 28, milk yield at first AI and cumulative milk yield to 120 days. Milk protein content was calculated on day 28 post partum, at nadir milk protein content and on the day of first AI. Liveweight and BCS were recorded at 24 h after calving and at first AI. Subsequent to the analysis of differences between strains and feeding systems, a number of retrospective analyses were carried out. All animals treated with hormones were removed from the data set at this point. The remaining data were divided into quartiles, based on the median values of the interval to CLA (<20 days, 20–26 days, 27–44 days and >44 days). The same data set was also retrospectively analysed by comparing cows with normal and abnormal progesterone profiles and by comparing cows which were pregnant or not to first AI.

2.9. Statistical analysis

The collated endocrine data were analysed using the mixed model described below using the statistical procedures of SAS [33]. Animals were blocked within strain and parity on calving date, pre-experimental milk yield, live-weight and body condition score. Since the basis for forming blocks was identical for all strains and strains were balanced on parity number, there would be expected to be some consistency in the block effects from strain to strain and should therefore be estimated as the consistent block effects across strains. Each lactation record was analysed separately in the current analysis. This model used is formally equivalent to a split-plot model:

$$R_{ijkl} = \text{mean} + S_i + L_j + (S \times L)_{ij} + B_k(S_i \times L_j) + F_l + (S \times F)_{il} + (L \times F)_{jl} + (S \times L \times F)_{ijl} + e_{ijkl}.$$

where R_{ijkl} = the response for the animal of strain i in lactation j on feed l; S_i = the effect of ith strain of HF ($i = 1$–3); L_j = parity ($j = 1$, p 2, 3), B_k = the consistent effect of block k within strain i by parity j interaction ($j = 1$–13); F_l = the effect of the lth feeding system ($k = 1$–3), and e_{ijkl} = the residual error term. The effect of strain of HF, parity and strain of HF by parity were tested using the block (strain of HF × parity) mean square as the error term. The effects of feeding system, the interaction of strain of HF × feeding system, the interaction of parity × feeding system, the interaction of parity × strain of HF × feeding system (the F_l, $S_i \times F_l$, $L_j \times F_l$ and, $S_i \times L_j \times F_l$ terms) were tested for significance using the residual mean square as the error term. The Student's t-test was used to determine the significance of differences between strains of HF and in the comparison of feeding systems MP versus HS and MP versus HC. Chi-square analyses were used to determine differences between the three strains, three feeding systems and the 2 years in the proportion of cows submitted in the first 24 days of the breeding season and conception rate to first service.

3. Results

Overall, feeding system or the interaction of strain of HF by feeding system did not significantly affect the traditional or endocrine fertility parameters measured, therefore the effects of strain of HF and parity are presented.

3.1. Traditional fertility parameters

The NZ strain had an earlier calving date, shorter gestation length and longer calving to service interval than both the HD and HP strains ($P < 0.05$) (Table 2). Both the HD (62%) and NZ (57%) strains had higher conception rates to first service than the HP strain (40%) ($P < 0.05$). There was no significant strain effect on 24-day submission rate, calving to conception interval or on days from calving to first observed oestrus. Strain of HF had no significant effect on the proportion of animals diagnosed as anoestrus by trans-rectal ultrasonography. Parity had no significant effect on reproductive performance.

Table 2
The effect of strain of Holstein-Friesian dairy cow ($n = 234$) on traditional fertility parameters

	HP	HD	NZ	S.E.M.	*P* value
Calving (day of year)	53^{a}	47^{a}	38^{b}	3.2	–[**]
Gestation length (days)	284^{a}	284^{a}	278^{b}	0.7	–[***]
Calving to first oestrus (days)	43.8	43.3	42.0	2.24	N.S.
Calving to first AI (days)	74.0^{a}	78.0^{ab}	85.3^{b}	2.97	–[*]
Calving to conception (days)	96.3	93.8	101.7	3.63	N.S.
Anoestrous cows (%)	10.3	9.0	6.4		N.S.
24-day submission rate (%)	78.2	85.9	88.5		N.S.
Conception to first service (%)	40^{a}	62^{b}	57^{b}		–[*]

Means with different superscripts within the same row are significantly different ($P < 0.05$). *P* values: N.S. = non-significant.

[*] $P < 0.05$.

[**] $P < 0.01$.

[***] $P < 0.001$.

3.2. Progesterone profiles

Strain of HF had no significant effect on CLA (Table 3). The mean CLA for all animals was 32.9 (S.E. 1.18) days, with the median of 27.3 days. CLA values ranged from 6 to 100 days with 42 and 85% of cows ovulating by day 26 and 60, respectively. The data were positively skewed (co-efficient of skewness of 1.18). Parity had an effect on CLA ($P < 0.001$). The CLA value for first lactation animals (46 days) was longer than for second (32 days) and third (31.1 days) lactation animals. The frequency distribution of CLA is displayed in Fig. 2. A total of 88 animals (37.6%) had one milk progesterone sample ≥ 3 ng/ml before the commencement of luteal activity with no significant difference between strains. The NZ strain had a shorter gestation length ($P < 0.05$) and

Table 3
The effect of strain of Holstein-Friesian dairy cow on postpartum luteal activity based on the analysis of milk progesterone concentrations

	HP	HD	NZ	S.E.M.	*P* value
CLA (days)	33.6	34.2	37.7	2.32	N.S.
CLA to AI interval (days)	41.5	44.2	48.3	2.73	N.S.
First luteal phase length (days)	13.7^{a}	14.3^{a}	11.4^{b}	0.83	–[*]
All luteal phase length (days)	14.3	14.0	13.5	0.52	N.S.
Luteal phases (No.)	2.28^{a}	2.39^{a}	2.77^{b}	0.122	–[*]
First IOI length (days)	21.7	22.3	20.1	1.03	N.S.
First ILI length (days)	7.4	7.8	7.9	0.63	N.S.
Atypical hormonal patterns (%)	39	34	42		N.S.
Transient progesterone rises (%)	32	40	40		N.S.
Early embryo mortality (%)	43	27	32		N.S.
Late embryo mortality (%)	17	11	11		N.S.

CLA: commencement of luteal activity, IOI: inter-ovulatory interval, ILI: inter-luteal interval. Means with different superscripts within the same row are significantly different ($P < 0.05$). *P* values: N.S. = non-significant.

[*] $P < 0.05$.

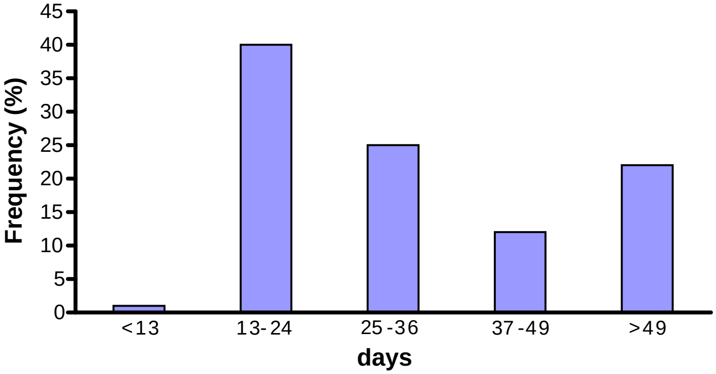

Fig. 2. Frequency distribution of interval to commencement of luteal activity (days) based on the analysis of milk progesterone profiles.

consequently had an earlier mean calving date ($P < 0.05$). The NZ group had more luteal phases ($P < 0.05$) because of their earlier calving date. Strain of HF had no significant effect on the percentage of cows displaying atypical hormonal patterns or the proportion of cows suffering early or late embryo mortality.

3.3. Effect of strain of HF on milk production, liveweight and BCS

Strain of HF had a significant effect on all milk production, liveweight and BCS variables (Table 4). The HP strain had the highest milk production at first AI, the NZ strain the lowest, while the HD strain were intermediate. The milk protein content at first AI was

Table 4
The effect of strain of Holstein-Friesian cow ($n = 232$) on milk production, liveweight (LW) and body condition score (BCS)

	HP	HD	NZ	S.E.M.	P value
Milk production					
Milk yield at day 28 (kg/cow/day)	30.1^a	30.0^a	27.5^b	0.45	$-^{***}$
Milk yield at first AI (kg/cow/day)	30.3^a	28.7^b	25.2^c	0.57	$-^{***}$
Milk protein content at first AI (g/kg)	32.3^a	33.1^b	34.3^c	0.03	$-^{***}$
Milk yield to 120 days (kg/cow)	3481^a	3335^b	3074^c	42.8	$-^{***}$
Liveweight					
LW at first AI (kg)	514^a	523^a	482^b	5.5	$-^{***}$
LW change post calving to first AI (kg)	−43.3	−35.4	−40.3	5.88	N.S.
Body condition score					
BCS at first AI	2.80^a	2.88^b	3.06^c	0.03	$-^{***}$
BCS change post calving to first AI	−0.27	−0.24	−0.23	0.03	N.S.

LW: liveweight, BCS: body condition score. Means with different superscripts within the same row are significantly different ($P < 0.05$). P values: N.S. = non-significant.

[***] $P < 0.001$.

Table 5
The effect of feed system ($n = 232$) on milk production, liveweight (LW) and body condition score (BCS)

	MP	HS	HC	S.E.M.	*P* value
Milk production					
Milk yield at day 28 (kg/cow/day)	28.6^{a}	28.4^{a}	30.5^{b}	0.44	–**
Milk yield at first AI (kg/cow/day)	27.8^{a}	25.7^{b}	30.8^{c}	0.42	–***
Milk protein content at first AI (g/kg)	33.0^{a}	32.8^{a}	33.9^{b}	0.03	–**
Milk yield to 120 days (kg/cow)	3237^{a}	3102^{b}	3550^{c}	37.1	–***
Liveweight					
LW at first AI (kg)	509^{ab}	498^{a}	513^{b}	5.0	–$^{+}$
LW change post calving to first AI (kg)	−44.7	−40.3	−34.0	4.08	N.S.
Body condition score					
BCS at first AI	2.94^{a}	2.85^{b}	2.95^{a}	0.03	–*
BCS change post calving to first AI	−0.31^{a}	−0.24^{b}	−0.19^{b}	0.03	–**

LW: liveweight, BCS: body condition score. Means with different superscripts within the same row are significantly different ($P < 0.05$). *P* values: N.S. = non-significant.

$^{+}$ $P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

highest with the NZ strain, lowest with the HP strain and intermediate with the HD strain. The highest liveweight at first AI was recorded with the HD strain, the lowest with the NZ strain, while the HP strain was intermediate. Strain of HF had no significant effect on liveweight change from calving to first AI. The NZ strain had the highest BCS at first AI, the HP the lowest, while the HD strain was intermediate. Strain of HF had no significant effect on BCS change from calving to first AI.

3.4. Effect of feed system on milk production, liveweight and BCS

Feed system had a significant effect on all milk production variables measured (Table 5). The HC group had the highest milk production, the HS group the lowest, while the MP group were intermediate. The milk protein content at first AI was highest with the HC group, and similar for both the MP and HS systems. The highest liveweight at first AI was recorded with the HC group, the lowest with the HS group, while the MP system was intermediate. Feed system had no significant effect on liveweight change from calving to first AI. The cows in the HS system had lower BCS at first AI compared to both the cows in the MP and HC systems. The cows in the MP system lost significantly more body condition from calving to first AI compared to the cows in the HC system with the cows in the HS system intermediate.

3.5. Associations between commencement of luteal activity and reproductive performance

Table 6 shows the effect of variation in interval to CLA on reproductive performance. Cows with the shortest interval to CLA (CLA <20 days; quartile 1) had the greatest number

Table 6

The effect of variation in the interval to commencement of luteal activity (CLA) on reproductive function (mean ± S.E.M.)

	Quartile 1 ($n = 45$)	Quartile 2 ($n = 45$)	Quartile 3 ($n = 49$)	Quartile 4 ($n = 47$)	P value
Commencement of luteal activity (days)	18.0 ± 1.26^{a}	24.6 ± 1.22^{b}	33.1 ± 1.15^{c}	58.6 ± 1.28^{d}	–***
Luteal phase (No.)	3.23 ± 0.20^{a}	2.79 ± 0.19^{a}	2.84 ± 0.16^{a}	2.08 ± 0.20^{b}	–**
CLA to AI (days)	58.4 ± 3.60^{a}	48.2 ± 3.56^{b}	45.5 ± 3.37^{b}	31.1 ± 3.65^{c}	–***
First luteal phase length (days)	13.7 ± 1.23	13.1 ± 1.21	13.4 ± 1.15	13.9 ± 1.26	N.S.
First interovulatory interval length (days)	23.5 ± 1.41	22.6 ± 1.39	20.6 ± 1.31	20.5 ± 1.47	N.S.
Abnormal hormonal patterns[†] (%)	18^{a}	24^{a}	6^{b}	3^{b}	–**
Transient progesterone rises (%)	31^{a}	20^{a}	47^{a}	77^{b}	–***
Mean calving day	47.8 ± 3.45^{a}	46.6 ± 3.36^{a}	43.1 ± 3.18^{a}	33.3 ± 3.52^{b}	–*
Calving to service (days)	75.8 ± 3.49^{a}	74.1 ± 3.40^{a}	77.3 ± 3.22^{a}	90.0 ± 3.55^{b}	–*
Calving to conception (days)	104.7 ± 6.32^{a}	82.0 ± 6.36^{b}	94.7 ± 5.94^{b}	105.1 ± 6.57^{a}	–*
Calving to first oestrus (days)	32.6 ± 3.06^{a}	37.7 ± 2.98^{a}	36.0 ± 2.82^{a}	52.9 ± 3.12^{b}	–***
24 day submission rate (%)	98	93	96	96	N.S.
Conception to first AI (%)	48.9	55.6	55.1	57.4	N.S.

Means with different superscripts within the same row are significantly different ($P < 0.05$). [†]Abnormal hormonal patterns.

P values: N.S. = non-significant here excludes delayed ovulation Type I.

[*] $P < 0.05$.

[**] $P < 0.01$.

[***] $P < 0.001$.

of luteal phases and the longest interval from CLA to AI. In contrast, cows with the longest interval to CLA (CLA >44 days; quartile 4) had the lowest number of luteal phases and the shortest interval from CLA to AI. With the exclusion of delayed ovulation type I (CLA >44 days) from the analysis, the frequency of abnormal hormone patterns was significantly lower in quartiles 3 and 4, while transient progesterone profiles did not differ between CLA quartiles. The mean calving date was later and the calving to service interval was longer for the fourth quartile (CLA >44 days; quartile 4) than for the other three quartiles. The calving to conception interval of both the first CLA quartile (CLA <20 days; quartile 1) and the fourth CLA quartile (CLA >44 days; quartile 4) were significantly greater than that of the other two quartiles. The calving to first observed oestrus of the cows with the longest interval to CLA (CLA >44 days; quartile 4) was significantly greater than the other three quartiles. Variation in interval to CLA had no significant effect on either conception rate to first service or 24 day submission rate. However, conception rate to first service for the cows in the first CLA quartile (CLA <20 days; quartile 1) was numerically lower than the other three groups. Commencement of cyclicity post partum (as measured by CLA) was not significantly affected by any of the milk production, liveweight or BCS variables (Table 7).

3.6. Associations between abnormal progesterone profiles and reproductive performance

Cows were retrospectively allocated to two categories: those that had normal ($n = 115$) and abnormal ($n = 71$) luteal profiles. Abnormal profiles for this analysis include DOVI (CLA $\geq$ 45 days post partum), DOVII (ILI $\geq$ 12 days), PCLI (first luteal phase length $\geq$19 days), and PCLII (subsequent luteal phases $\geq$19 days). The results of this analysis are displayed in Table 8. Cows with abnormal luteal activity had a later CLA ($P < 0.001$), fewer luteal phases ($P < 0.01$) and a shorter interval from CLA to AI ($P < 0.01$). The abnormal group also had a longer first luteal phase length ($P < 0.05$) and greater first inter-ovulatory interval ($P < 0.05$). Similarly, cows with abnormal luteal activity had an earlier calving date ($P < 0.05$), longer calving to first service interval ($P < 0.05$) and a longer interval from calving to first observed oestrus ($P < 0.001$) when compared to cows with normal luteal activity. There was no significant difference in either 24-day submission rate or conception rate to first service for cows with normal and abnormal luteal activity. There was no significant difference between cows displaying normal and abnormal progesterone profiles in terms of milk production, liveweight and BCS (Table 9). Parity had a significant effect on the proportion of animals with atypical hormone patterns. More atypical patterns ($P < 0.001$) were observed among primiparous animals (62%) than with pluriparous animals (44%).

3.7. Associations between endocrine parameters and conception success at first AI

Cows were retrospectively allocated to two categories: those pregnant to first service ($n = 101$) and non-pregnant to first service ($n = 85$). There was no significant difference in luteal activity between pregnant and non-pregnant cows (Table 10). There was no significant difference in calving date or calving to service interval between cows pregnant and non-pregnant to first service. As expected, cows non-pregnant to first service had a

Table 7
The effect of variation in the interval to commencement of luteal activity on milk production, liveweight and body condition score in early lactation (mean ± S.E.M.)

	Quartile 1 ($n = 45$)	Quartile 2 ($n = 45$)	Quartile 3 ($n = 49$)	Quartile 4 ($n = 47$)	P value
Milk production					
Milk yield on day 28 (kg/cow/day)	28.6 ± 0.65	29.8 ± 0.71	28.7 ± 0.67	29.4 ± 0.74	N.S.
Milk yield at first AI (kg/cow/day)	28.3 ± 0.68	28.1 ± 0.66	28.8 ± 0.63	27.9 ± 0.69	N.S.
Milk protein content: first AI (g/kg)	32.9 ± 0.04	33.2 ± 0.04	33.0 ± 0.03	34.0 ± 0.04	N.S.
Nadir milk protein content (g/kg)	30.5 ± 0.05^{a}	30.6 ± 0.05^{a}	29.2 ± 0.04^{b}	29.3 ± 0.05^{ab}	–[*]
Milk yield to 120 days (kg/cow)	3264 ± 60.7	3315 ± 59.1	3309 ± 56.2	3334 ± 62.9	N.S.
Liveweight and BCS					
LW at first AI (kg)	509 ± 7.6	501 ± 7.4	505 ± 7.0	515 ± 7.7	N.S.
LW change from calving to first AI (kg)	−42.2 ± 6.39	−51.9 ± 6.22	−38.5 ± 5.88	−31.9 ± 6.50	N.S.
BCS at first AI	2.95 ± 0.04	2.90 ± 0.04	2.92 ± 0.04	2.91 ± 0.05	N.S.
BCS change from calving to first AI	−0.21 ± 0.04	−0.28 ± 0.04	−0.26 ± 0.04	−0.29 ± 0.04	N.S.

LW: liveweight, BCS: body condition score. Means with different superscripts within the same row are significantly different ($P < 0.05$). P values: N.S. = non-significant.

[*] $P < 0.05$.

Table 8
Differences in endocrine and fertility parameters for cows with normal and abnormal ovarian activity post partum (mean ± S.E.M.)

Profile category	Normal ($n = 115$)	Abnormal ($n = 71$)	P value
CLA (days)	26.9 ± 1.92	46.9 ± 2.29	–***
Luteal phases (No.)	3.01 ± 0.13	2.26 ± 0.15	–**
CLA to AI (days)	49.5 ± 2.63	37.5 ± 3.13	–**
First luteal phase length (days)	12.2 ± 0.77	15.3 ± 0.93	–*
First interovulatory interval (days)	20.2 ± 0.91	23.2 ± 1.11	–*
Calving (day of year)	46.1 ± 2.23	36.8 ± 2.69	–*
Calving to first oestrus (days)	35.3 ± 2.03	47.4 ± 2.45	–***
Calving to service (days)	75.6 ± 2.26	85.4 ± 2.72	–*
Calving to conception (days)	95.5 ± 4.11	97.5 ± 4.99	N.S.
24-day submission rate (%)	96	96	N.S.
Conception rate to first service (%)	53	56	N.S.

CLA: commencement of luteal activity. P values: N.S. = non-significant.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

longer calving to conception interval ($P < 0.001$) than cows pregnant to first service. There was no significant difference between the two groups in the interval from calving to first observed oestrus or 24-day submission rate.

4. Discussion

Measures of the interval between calving and CLA, determined using milk progesterone profiles, have been suggested as suitable selection criteria for fertility [23–25]. The North

Table 9
Differences in milk production, liveweight and body condition score for cows with normal and abnormal ovarian activity post partum (mean ± S.E.M.)

Profile category	Normal ($n = 115$)	Abnormal ($n = 71$)	P value
Milk production			
Milk yield at day 28 (kg/cow/day)	29.3 ± 0.46	29.0 ± 0.56	N.S.
Milk yield at first AI (kg/cow/day)	28.8 ± 0.42	27.6 ± 0.51	N.S.
Milk protein content at first AI (g/kg)	33.2 ± 0.03	33.4 ± 0.03	N.S.
Milk yield to 120 days (kg/cow)	3324 ± 38.5	3287 ± 47.3	N.S.
Liveweight			
LW at first AI (kg)	507.2 ± 4.8	509.9 ± 5.8	N.S.
LW change from calving to first AI (kg)	−43.9 ± 4.11	−36.1 ± 4.96	N.S.
Body condition score			
BCS at first AI	2.93 ± 0.03	2.91 ± 0.03	N.S.
BCS change from calving to first AI	−0.25 ± 0.02	−0.27 ± 0.03	N.S.

LW: liveweight, BCS: body condition score. P values: N.S. = non-significant.

Table 10
Endocrine and fertility parameters for cows that were pregnant and non-pregnant to first AI ($n = 186$)

Reproductive status	Pregnant ($n = 101$)	Non-pregnant ($n = 85$)	P value
CLA (days)	35.9 ± 2.24	34.6 ± 2.23	N.S.
CLA to AI (days)	44.4 ± 2.76	44.8 ± 2.75	N.S.
First luteal phase length (days)	14.4 ± 0.82	12.7 ± 0.81	N.S.
Abnormal profiles (%)	39.6	36.5	N.S.
Calving (day of year)	40.1 ± 2.44	44.1 ± 2.43	N.S.
Calving to first oestrus (days)	41.3 ± 2.31	39.6 ± 2.29	N.S.
Calving to service (days)	80.7 ± 2.49	78.9 ± 2.48	N.S.
Calving to conception (days)	78.1 ± 3.57	115.9 ± 3.72	–[***]
24-day submission rate (%)	97	94	N.S.

CLA: commencement of luteal activity. P values: N.S. = non-significant.
[***] $P < 0.001$.

American HF has been selected for increased milk yield in a predominantly feedlot environment [34]. In contrast, the New Zealand HF has been selected for milk production, feed efficiency and survivability on a predominantly grass-based diet with very little concentrate supplementation [35]. Therefore, this dataset provides a unique opportunity to investigate the relationship between luteal function post partum and reproductive performance across three strains of Holstein-Friesian cows selected with very different breeding objectives on three different pasture-based feeding system.

4.1. Effect of strain of Holstein-Friesian on traditional and endocrine fertility parameters

In both years the NZ strain had longer calving to service interval than both the HP and HD strains because of the shorter gestation length while AI commenced on a fixed date (20 April). The higher conception rates to first service for both the HD and NZ strains compared to the HP strain was predicted from the superior PDs for survival and calving interval of the sires used to generate these strains [14]. The non-significant effect of feeding system on reproductive performance is consistent with results obtained previously at this institute [10,11]. In the present study the interval to CLA was similar for all three strains. In New Zealand a similar study showed that North American HF had a shorter interval to CLA than New Zealand HF cows [36]. In that New Zealand study a much higher percentage of cows were treated for anoestrus (43%) than in the present study (8.5%). This may account for the discrepancy between studies. The mean interval to CLA of 32.9 (S.E. 1.18) days obtained in the present study is greater than that obtained by [29] (27.4–27.9 days) and [24] (29.5 days). In the present study the mean length of the first IOI (21.0 ± 7.2 days) was similar to that reported by [37] (22.2 ± 8.7 days). [29] reported a similar interovulatory interval for modern day Holstein-Friesian dairy cows (1995–1998; 22.5 ± 10.8 days). This was significantly longer than that of cows in the preceding 20 years (18.9 ± 7.5 days). [29] suggested that the longer IOI in the modern HF cow might reflect slower blastocyst growth leading to later interferon production since animals with early luteolysis and slow conceptus growth lose their pregnancies.

4.2. Effect of feed system on traditional and endocrine fertility parameters

Feed system had no significant effect on any of the traditional or endocrine fertility variables analysed. This is in agreement with results from previous long-term selection studies at this institute [10,11,38]. These studies have shown that when animals receive sufficient quantities of high quality pasture, increasing the energy density of the diet through concentrate supplementation does not result in improved reproductive performance. The hypothesis in the present study was that the cows in the HC system would be in less severe negative energy balance in early lactation and would return to positive energy balance at an earlier stage of lactation than the cows in the HS system. The higher milk production and relatively small differences in liveweight and BCS change from calving to AI between feed systems, suggests that much of the additional concentrate was partitioned to increase milk production and therefore did not lead to improved reproductive performance.

4.3. Associations between commencement of luteal activity and reproductive performance

Early re-establishment of ovarian activity has been favourably associated phenotypically with fertility [7]. Cows that started cycling early had a reduced interval to conception through having a higher chance of early insemination post partum, higher conception rate and fewer services per pregnancy than those with a prolonged anovulatory period. A number of authors have concluded that conception rates increase with each additional oestrous cycle before service [39,40]. However, in the present study very early ovulation after calving (CLA <20 days; quartile 1) was associated with an increased calving to conception interval. A number of more recent studies would support this finding [29,41,42]. Similarly, [43] showed that early ovulation post partum was detrimental to conception in the lactating ewe, because luteal activity may occur before the uterus has undergone complete involution. A reason for the poorer conception rates could be due to a higher incidence of uterine infection with very early ovulation post-partum.

4.4. Associations between abnormal hormonal patterns and reproductive performance

A normal progesterone profile was defined as the resumption of luteal activity by day 45 post partum and cycling at regular intervals of 21 days [18]. The incidence of abnormal hormonal patterns observed in this study (38.3%) is slightly less than that reported by [29], (44%) for modern Holstein-Friesian cows, and greater than that observed between 1975 and 1982 by [44]. Although the exact pathways are not understood, it has been clearly demonstrated that the duration and intensity of NEB post partum has a major impact on ovarian function [45,46]. In the present study, there was no significant difference between cows with normal and abnormal progesterone profiles in terms of milk production liveweight or BCS, and so no effect of energy balance post partum could be detected. Although cows with abnormal progesterone profiles did not have reduced conception rates to first insemination, they did have a longer calving to first service interval. The data collected in this study indicate that abnormal progesterone profiles did not have significant negative effects on fertility. The incidence and effect of abnormal profiles within this study suggest that the criteria used to classify abnormal profiles needs to be redefined.

4.5. Associations between endocrine parameters and conception to first service

In the present study there was no significant difference in endocrine or fertility parameters between cows that were pregnant and not pregnant to first service. This indicates that postpartum follicular development did not contribute to differences in conception rate to first AI between strains. Recent results from this institute showed that oocyte quality in the HP cows might have been impaired, resulting in lower conception rates [47]. The probability of conception may be negatively associated with the magnitude and duration of NEB in early lactation [40,48,49]. Cows of high genetic merit for milk production are associated with more severe NEB [10,11,50–52] and this may result in poorer oocyte quality and reduced reproductive performance.

5. Conclusion

Strain of Holstein-Friesian did not influence on the interval to commencement or subsequent pattern of ovarian activity, but did influence conception rate to first service. Feed system had a significant effect on milk production but did not influence endocrine activity or reproductive performance. These data show that when animals receive sufficient quantities of high quality pasture, increasing the energy density of the diet through concentrate supplementation does not result in improved reproductive performance. The results also show that very early ovulation post partum (CLA <20 days) is associated with a prolonged calving to conception interval. Cows with abnormal progesterone profiles had similar milk production, liveweight, and body condition score to cows with normal progesterone profiles. The results of the present study also show that postpartum progesterone profiles did not differ between cows pregnant and not pregnant to first service.

Acknowledgements

This study is part of a joint project between Dexcel (New Zealand), Massey University (New Zealand), and Teagasc (Moorepark). We would like to acknowledge the support of Professor Colin Holmes (Massey University). The authors acknowledge L.I.C. for sponsoring the New Zealand embryos. We thank the staff of Curtins farm for their co-operation, care and management of the experimental animals.

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