Identifying Heritable Endocrine Parameters Associated with Fertility in Postpartum Dairy Cows

A.O. Darwash[1], G.E. Lamming[1] and J.A. Woolliams[2]

[1]Cattle Fertility Research Group, University of Nottingham, Sutton Bonington, Loughborough LE12 5RD, UK
and
[2]Roslin Research Institute, Roslin, Midlothian EH25 9PS, Scotland, UK

Abstract

Attempts to improve the reproductive efficiency in dairy cattle through breeding and selection have been frustrated by the lack of heritable reproductive parameters conducive to high fertility. The traditional fertility parameters of interval to first service, services per conception, days open and calving intervals are highly influenced by managerial decisions and are expected to have heritabilities too low to permit a meaningful genetic gain through selection. Another approach is to use the growing body of evidence that the majority of endocrine and physiological factors affecting reproduction are a result of gene expression at the hypothalamic, pituitary ovarian or uterine axis. In order to investigate this, two research studies are being conducted with the aim of estimating the genetic component of the variation between dairy animals in the postpartum reproductive patterns. Furthermore, the association between a particular endocrine or physiological pattern and subsequent fertility is being analysed. Based on data we have analysed to date, the early return to postpartum cyclicity and corpus luteum competence following a timely service were found to be significantly correlated with high conception. The early return to ovarian cyclic pattern after calving was found to be heritable (h^2=0.21, P<0.05), while the inter-luteal interval, which indicates timely ovulation, was repeatable (r^2=0.094, P <0.01). The next phase of the analyses will quantify the association between the incidence of atypical ovarian patterns and the inherited differences in the sensitivity to GnRH.

1. Introduction

Animal breeders and geneticists have successfully used reproductive techniques such as artificial insemination (AI) and multiple ovulation and embryo transfer (MOET) to propagate the genetic merits of dairy animals. The heritability (h^2) for milk yield estimated from 25% (Bourdon, 1997) to 35% (Swalve, 1995), coupled with improved nutritional and managerial practices, have resulted in a dramatic increase in the annual milk yield of the dairy cow. However, this improvement in the production capacity of the dairy cow has not been accompanied by an improved reproductive efficiency, in fact the reverse. As it is shown in Fig. 1, conception rate to a particular service in the US was reduced by approximately 1% for every 2.5 years between 1960 and 1995 (Butler& Smith, 1989; Butler *et al*., 1995; Butler, 1997). Although no comparable reliable figures are currently available for UK herds, the trend is expected to be similar, as an extensive breed substitution has taken place through a large importation of Holstein-Friesian genetic material from the US and other sources. This decline in fertility has raised concern since the cost of subfertility is negatively affecting profit margins in a highly competitive market for milk, as it is increasingly the case in the EU. This trend will increase if milk quotas were removed. The effect of high milk yield on fertility has been controversial, since a number of workers have found a negative genetic correlation between production and reproduction (Hansen *et al*., 1983; Faust *et al.,* 1988; Oltenacu *et al*. 1991), while contrary to these findings, no effects of high milk yield on the reproductive efficiency (Nieuwhof *et al.,* 1990), ovarian function (Harrison *et al.,* 1990) or on the interval to postpartum ovulation (Darwash *et al*. 1997[a]) were observed in postpartum dairy cows. However, (Hermas *et al*, 1987; Seykora & McDaniel, 1983; Philpson, 1981) went further to state that a substantial additive genetic variance does exist and that profitable breeding programmes should include selection for reproductive traits.

1.1 Fertility of the postpartum cow

As a quantitative trait, fertility is influenced by a number of environmental, nutritional, managerial and endocrine factors. In order for a cow to conceive and maintain pregnancy, it is imperative that synchrony is achieved between a number of physiological and managerial processes and that managerial practices do not prejudice this being achieved. These currently include a visible manifestation of oestrus, a timely natural mating or alternatively artificial insemination (AI) by skilled technicians using semen of fertile bulls; shedding of an ovum capable of being fertilized and the secretion of adequate progesterone levels essential for optimum tubal and uterine environments to maintain the developing embryo. There is an increasing awareness that the current practices of assessing the genetic variation in fertility by monitoring parameters such as interval to first service, interval to conception, and services per conception are expected to produce low heritabilities < 0.1 (Hays *et al*., 1992; Campos *et al.,* 1994; Marti & Funk, 1994) and are inaccurate measures of the cow's inherent abilities, since they are to a large extent, masked by managerial practices (Woolliams, 1997). One of the main factors contributing to this situation is the unavailability of reliable endocrine and physiological measurements that are more accurately associated with the inherent status of the animal fertility which could then be amenable to genetic analysis.

1.2 The rate of genetic progress for selected traits

The low heritability levels reported for traditional measures of fertility have lead many to believe that selection for fertility or discriminating against subfertility are equally futile practices. This was exacerbated by the expected emphasis on milk yield which results in culling fertile animals that are low producers while giving every opportunity for subfertile animals (with delayed first PP service, higher number of services and delayed interval to postpartum conception) to remain in the herd and therefore, produce the next generation of cows. In our opinion, this is one of the main management practices contributing to the persistent decline in „fertility“ level as we select for high yield. The existence of the negative genetic correlation does not mean that it is unavoidable, as properly-managed high producers have been reported to be highly fertile, and so we need to develop better tools than we have at present. **Our objective in this study is to promote an alternative philosophy of moving towards identifying genetic variation in fertility traits that reflect the inherent endocrine and physiological capacity of the dairy cow; thus providing the possibility of using objective and reliable measuring techniques.**

2.0 Materials and Methods

In order to obtain meaningful estimates of genetic parameters for physiological or endocrine traits, a well-structured study with sufficient numbers of animals monitored, using accurate and objective measures is needed. The on-going data collection will be described but the results will be presented from data collected on British Friesian cows between 1975-1982 which was described in detail by Darwash *et al* 1997[a,b].

2.1 Animal database for the milk progesterone monitoring

Milk progesterone measurements on samples collected thrice-weekly from shortly after calving until 30 days post insemination in 2400 animals during 3500 lactations will be used for identifying endocrine patterns conducive to high fertility. Out of these, an on-going study covering 900 Holstein-Friesian animals of 65 sires families raised in 6 farms between 1995-1998 has been specifically structured for the estimation of genetic variation between postpartum dairy cows with regard to a number of endocrine and physiological traits.

2.2 Endocrine and physiological traits monitored

Using the model shown in Fig. 2, coupled with field observations and heat mount detectors the following parameters are being measured:

- Interval to postpartum ovulation
- The incidence of silent ovulation
- Intensity of oestrus
- Corpus Luteum competence
- Incidence of delayed luteolysis
- Incidence of delayed ovulation
- Conception and pregnancy rates
- Early and late embryo mortality

In addition to above traits, milk yield and calving type are being recorded.

2.3 Defining luteal activity

Two consecutive readings of P_4 levels > 3ng/ml, in a thrice-weekly sampling routine, have been used to indicate the presence of luteal activity.

2.4 Defining typical and atypical ovarian patterns

In order to identify qualitative differences between extremes, all luteal phases having measurements up to 1 s.d. above the mean were considered as typical. The continuous variation found between cycles was used to identify and quantify the incidence of atypical traits (e.g. delayed ovulation and delayed luteolysis) within and between lactations. The first stage in the analysis covered all data collected from the field including hormonal treatments whose effects can not be easily quantified from field observations. The second stage was to limit the analyse to spontaneously occurring events in untreated animals. This approach has introduced a bias in measurements since the majority of treated animals were with extreme cycle measurements. Following the definition of luteal activity, the incidence of atypical patterns were based on the number of lactations studied. The incidence of late embryo mortality was calculated from lactations where insemination or natural mating have taken place. In the on-going data collection for the genetic trials, no hormonal treatment was allowed between calving and day 80 postpartum.

In order to decrease errors arising from using field data in characterizing reproductive parameters, an attempt was made to introduce objective measures that can be validated.

2.5 Measuring the occurrence of oestrus

The incidence of oestrous behaviour is generally expected within 48 hours following the demise of the CL. In addition to the visual routine checks by experienced herdsmen, KMAR® (HEATMOUNT™ DETECTORS, supplied by Kmar, inc., Steamboat Springs, CO 80477), are used on cows included in the genetic trials. These were routinely changed after each positive reading.

2.6 Scoring the intensity of oestrus

Depending on the degree of oestrous manifestation and KMAR results, two scores of 1-3 are given to the intensity of heat by the herdsman and the inseminator. The average of both scores is used to indicate the intensity of heat.

2.7 Measuring the incidence of silent ovulation

If oestrus, using above methods, was not detected within 12 days before P4 rise > 3ng/ml, the respective ovulation would be considered as silent.

2.8 Luteal phase characteristics

In order to investigate the variation between animals in the luteal activity, intervals shown in Fig. 3 were characterized.

A Oestrus to P4 rise (> 3ng/ml)
B Luteal phase length
C Oestrus to peak P4 levels
D Peak P4 to the demise of the CL
E The interval between two oestrous

periods

2.9 Measurement of progesterone concentrations in milk samples

Milk progesterone concentrations were measured in un-extracted aliquots of whole milk using Radioimmunoasssay, validated at the University of Nottingham Laboratories, or ELISA techniques, using plates and procedures recommended by Ridgeway Science Ltd. (Rodmore Mill Farm, Alvington, Gloucestershire GL 15 6AH, UK). Samples were re-assayed if the CV of duplicate samples was > 15% between P_4 values of 1.5-10.5 ng/ml milk.

2.10 Experimental design

A design was chosen to be close to the optimum for a half-sib design (Robertson, 1959 & Swiger, *et al*. 1964).

2.11 Statistical analysis

Existing data has been analysed using ASREML software. Fixed effects include parity, calving season, herd and year. The random model estimates the genetic variance using the known pedigrees.

3.0 Results

3.1 Typical and atypical postpartum ovarian patterns

In analysing data of the first study (Lamming & Darwash, 1995; Darwash and Lamming, 1995), it was shown that following the first postpartum ovulations (n=2349), milk progesterone profiling of subsequent cycles may be characterized, as a series of luteal (n=10009) and inter-luteal intervals (n= 5219). Results of characterizing atypical luteal patterns using milk P_4 levels are presented in Table 1. Delayed ovulation indicates the various stages of cystic follicle formation; while delayed luteolysis results in a persistent corpus luteum in the cyclic animals. Subsequent to natural or artificial service, delayed luteolysis may denote the occurrence of late embryo mortality.

3.2 The incidence of atypical ovarian patterns

The incidence of atypical ovarian patterns found in treated and untreated animals is shown in Table 2.

3.3 The return to cyclic pattern after calving

The mean interval to postpartum luteal activity during 2349 lactations in the database analysed to date was 28.7 ±14.6 days (□ ±s.d.). Based on this, P4 rise (> 3ng/ml) observed during 257 lactations (10.94%) after day 44 (> 28.7+14.6 days) PP was considered a result of delayed ovulation type I (DOVI). Since it was not possible to quantify the effects of hormonal treatments from field trials, analysis of the association between the interval to postpartum ovulation and measures of fertility was limited to animals that received no remedial veterinary treatment for reproductive disorders. In this untreated group, the average interval to PP P_4 rise was 27.0 ±12.1 days,

Table 1. Defining atypical luteal activity using milk P_4 levels

Atypical reproductive pattern	Definition
Delayed Ovulation type I (DOVI)	P_4 levels (< 3ng/ml) for longer than 44 days PP
Delayed Ovulation type II (DOVII)	P_4 levels (< 3ng/ml) for longer than 12 days between two cycles.
Delayed Luteolysis during first cycle, Persistent corpus luteum type I (PCLI)	P_4 levels (> 3ng/ml) for longer than 19 days during the first postpartum cycle.
Delayed Luteolysis during subsequent cycles without insemination, Persistent corpus luteum type II (PCLII)	P_4 levels (> 3ng/ml) for longer than 19 days during subsequent postpartum cycle.
Late embryo mortality (LEM), embryonic death after day 16 post service	P_4 levels (> 3ng/ml) for longer than 19 days following natural or artificial service.

PP Postpartum P_4 Progesterone

Table 2. The incidence of atypical ovarian patterns in 1683 PP cows during 2503 lactations as defined by milk P_4 profiles *

Atypical pattern	No.	%
Delayed ovulation Type I	257	10.94
Persistent CL Type I	169	7.3
Persistent CL Type II	159	6.35
Delayed ovulation Type II	322	12.85
Late embryo mortality	238	9.92[a]
Total number of lactations with one or more types of atypical pattern	930	37.2

*Taken from Darwash and Lamming 1997.

[a] Quantifying the incidence of late embryo mortality was based on a total of 2400 lactations where natural or artificial service were performed.

(n=1733) indicating an interval to postpartum ovulation of 21.3 days (27-5.7) (Darwash *et al.* 1997[a]). In this group, there was a significant effect ($P<0.001$) of season on the interval to PP ovulation with the shortest (23.1 days) being in autumn and the longest (27.9 days) in summer. The interval to PP ovulation became progressively longer ($P<0.001$) as the number of parities increased.

3.4 Luteal phase length

The luteal phase length (P_4> 3ng/ml) of 5519 cycles in untreated animals averaged 12.9±6.6 days (μ ± s.d.). The spontaneously occurring luteal activity in these animals showed a gradual PP recovery. The length of the luteal activity has increased from a mean of 10.64 days (n=1715) observed during the first cycle to 13.1 days (n=1588), 14.32 (n=1116) and 14.85 days (n=550) during the second, 3rd and 4th postpartum cycle, respectively. The incidence of delayed luteolysis, with cycles having luteal activity longer than 19 days is tabulated in Table 2.

3.5 Variation between animals in luteal phase characteristics

In order to characterize the spontaneously occurring luteal activity and to reduce the magnitude of error arising from infrequent sampling, a total of 331 „untreated“ cycles, monitored daily, which were not preceded by AI or natural mating, have been analysed. The various stages of the luteal phase characterized are tabulated in Fig 3. Since we have no measure to assess the luteal phase competence, the mean and standard deviations of the various luteal phase components tabulated in Table 3, show the extent of the variation found between cycles.

Table 3. Variation between cycles in luteal phase characteristics (321 untreated, daily monitored cycle).

Parameter	Mean	s.d	No.
Interval from oestrus to P_4 rise, days	6.27	2.05	89
Interval from oestrus to peak P_4, days	14.44	4.43	90
Interval from oestrus to CL demise	19.67	3.21	82
Interval between two oestrous periods	20.94	3.48	62
Peak P_4 levels, ng/ml milk	36.17	16.91	302[1]
Interval from Peak P_4 to the CL demise	5.24	2.82	298[1]

P_4 Progesterone CL Corpus luteum

[1] The numbers include cycles with silent ovulation.

3.6 The inter-luteal interval

The inter-luteal interval (ILI) is a new term which we have introduced into the literature in 1995. It covers the period between the demise of the CL and the rise in progesterone levels (P_4 > 3ng/ml) of the next cycle (see Fig. 4 taken from Lamming and Darwash, 1995). Since we believe that the only meaningful endocrinological bench mark in the cycle is the day of the CL demise, for this analysis all cycles were normalized using this day as an indicator for the timely ovulation and or CL competence. In the untreated group, ILI had a mean length of 7.8 ±4.3 days (n=5204 cycles). In this study inter-luteal intervals of > 12 days found in 12.85 % of animals during 2503 lactations were considered a result of delayed ovulation type II.

3.7 Late embryo mortality

On-average, embryonic death prior to day 16 in the cow does not result in delaying luteolysis. In this study delayed luteolysis (luteal activity > 19 days) after mating or natural service , which may be a result of late embryo mortality (after day 16), has been observed in 238 (9.9%) out of 2400 inseminated or naturally mated animals.

3.8 The incidence of silent ovulation

It was not possible to analyse all existing field data (collected during 1975-1982 from 20 farms) for such a highly subjective trait, as heat detection depends on the cow's ability to manifest visible symptoms of oestrus as well as on the herdsman's efficiency to detect heat. However, data collected on dairy cows raised on the University of Nottingham research farm (1978-1982) offer a unique opportunity to quantify the incidence of this trait. The cows were daily monitored from shortly after calving until the confirmation of the reproductive status of the animal (usually 100 days after service) and heat detection was practised as of day 0 post calving. Using daily milk progesterone levels to quantify the expected occurrence of oestrus, the incidence of silent ovulation in individual cows was found to range from 0% to 100% during the lactations studied. In 337 cycles when the animal received no treatment for reproductive hormones, the incidence of silent ovulation was respectively, during the first, second, third and fourth cycles, 80.95% (n=84), 56.25% (n=96), 34.12% (n=85) and 27.78% (n=72).

3.9 Atypical ovarian patterns and fertility

As it is shown in Table 4 animals showing one or more atypical ovarian patterns, as defined in Table 1, have lowered reproductive performance and higher incidence of veterinary intervention. Furthermore, atypical ovarian activity was also found to be conducive to higher incidence of early (lower conception rates) and late embryo mortality. Although the differences between the two groups of animals were highly significant, the level of significance was not quoted here due to the difficulty in quantifying the effects of veterinary intervention from field data. The group with the atypical ovarian patterns had higher milk yield, indicating possible effects of high yield on the incidence of certain atypical ovarian patterns. In this regard some caution is needed in the interpretation of these results as it was not possible to find appropriate correction factors to adjust yield for lactation length or number.

3.10 The Heritability and Repeatability of typical and atypical ovarian patterns

3.10.1 Heritability of the interval to postpartum ovulation

Shorter intervals to postpartum ovulation were favourably correlated with measures of fertility; such that for every day delay in the interval to ovulation there was an average delay of 0.24 and 0.41 days ($P<0.001$) in the interval to first service and conception, respectively. The number of services per conception was reduced 0.11($P<0.001$) for every additional 21 day between between the interval to postpartum ovulation and first service (Darwash et al 1997[b]).

Furthermore the interval to postpartum ovulation within a population of Friesian cows in the UK was heritable ($h^2=0.21$; $P < 0.05$) and repeatable($r^2=0.26$, $P<0.01$).

3.10.2 Heritability and repeatability of inter-luteal intervals

The length of the inter-luteal interval (ILI), in 1353 untreated animals during 1856 lactations, was significantly ($P <0.001$) correlated with subsequent luteal phase activity in cycling animals and with conception rate in the mated cows. Conception rates to a particular service decreased from 71.7% to 44.2% respectively, for ILIs of 4-8 and 9-13 days. The repeatability of this essential trait between cycles within a lactation was $r^2=0.094$, $P< 0.01$. The variation between cows raised in the various herds was significant ($P < 0.05$) while cows during later parities have significantly($P<0.01$) longer inter-luteal intervals.

3.10.3 Heritability and repeatability of other atypical traits

The ongoing structured-studies will have the necessary data for reliable estimates of the genetic variation in cycle length, the incidence of silent ovulation, intensity of oestrus, early and late embryo mortality, synchrony between oestrus and ovulation, luteal phase characteristics and the covariation with milk yield, which is being recorded on regular basis, and the sensitivity to GnRH challenge in dairy animals.

Table 4: Effects of atypical ovarian patterns on reproduction in postpartum (PP) cows

	Lactations with typical cycles (n=1573)			Lactations with atypical cycles (n=930)		
Parameter	Mean	No.	SE	Mean	No.	SE
Days to lst. PP service	71.8	1520	0.51	77.8	880	0.82
Days to conception	83.1	1427	0.76	113.6	717	1.82
First service conception, (%)	(66.4)	1009		(37.1)	326	
Total conception, %	(94)	1427		(81.5)	717	
Treated with reproductive hormones, (%)	(15.6)	244		(34.4)	322	
Milk Yield, kg, (300-305 days)	5692.4	535	31.2	5940	369	58.8

4. Discussion

4.1 Progesterone during the oestrous cycle and early pregnancy in the cow

Following ovulation, which normally occurs 6-12 hours after oestrus, the rapidly growing corpus luteum (CL) is formed. One of the main functions of the CL is to secrete progesterone which is measurable in blood and milk. During a 21-day cycle, there should be on-average, 14-15 days (between days 4-19) where the animal shows measurable P_4 levels > 1 ng/ml in plasma or >3ng/ml in milk. Following the demise of the CL, a period of 6-7 days is characterized by low P_4 levels (< 3ng/ml in milk). Progesterone profiling allows ovarian activity to be characterized into luteal and inter-luteal periods (ILIs). This form of characterizing ovarian activity is much more objective and accurate than the inter-ovulatory or inter-oestrual intervals commonly used in most research projects; since neither ovulation nor behaviour at oestrus can be accurately measured with the objectivity required. Furthermore, the day of CL demise can be used as a benchmark to normalize oestrous cycles for analysis, and not the currently used day of ‘oestrus’.

The interval between the demise of one CL and the rise of another is extremely important in determining whether there was the desired synchrony between the various mechanisms controlling luteolysis, follicular development and selection, ovulation and timely P_4 secretion . Furthermore, the length of ILI verifies whether AI was timely in relation to ovulation (Darwash & Lamming, 1996). The presence of P_4 profiles will assist in validating all fertility parameters for the genetic analysis as it will separate managerial failure from that of the cows' endocrine incompetence in the lowered fertility observed in certain cows.

4.2 The role of atypical hormonal patterns in subfertility

As it is shown in Table 4, atypical ovarian patterns are a major factor causing a delay in conception through higher rate of early and late embryo mortality. Furthermore subfertility reduces the production efficiency through higher culling rate, reduced production and higher cost of veterinary intervention and additional inseminations. The high incidence of silent ovulation observed in some cows causes animals to be unnecessarily submitted for veterinary treatments and inseminated at an inappropriate time in relation to ovulation. In this study, shorter intervals to postpartum ovulation and early progesterone rise after insemination were identified as being favourably correlated with high fertility in postpartum dairy cows.

4.3 Etiology of atypical ovarian patterns

The asynchrony between the various mechanisms controlling the oestrous cycle and early pregnancy may be a result of GnRH insufficiency or the sensitivity of its receptors in target organs, which require a further extensive study.

4.4 The genetic improvement of fertility traits

If sufficient additive genetic variation is found in one or more of the reproductive traits currently being studied, and if such trait was genetically associated with fertility, then selection for or discriminating against such parameter is expected to result in a genetic gain.

5.0 Conclusion

There is a need to identify fertility parameters with sufficient additive genetic variation to be included in future selection indices of dairy animals. Milk progesterone monitoring offers objective and accurate measures for identifying heritable endocrine parameters and their association with improved reproductive performance.

In the past, geneticists and animal breeders have used reproductive techniques to improve the genetic merits for yield. In the future, genetic knowledge should be used to improve the reproductive efficiency of dairy cows.

References

Bourdon, R.M. Understanding animal breeding. Prentice Hall, N.J. pp 523

Butler, W.R. and Smith, R. D. 1989. Interrelationship between energy balance and postpartum reproductive function in dairy cattle. J. Dairy Sci. 72:767-783.

Butler, R.W., Cherney, D.J.R and Elrod, C.C. 1995. Milk urea nitrogen (MUN) analysis: field trial results on conception rates and dietary inputs. Proceedings of the Cornell Nutrition Conference, Rochester, N.Y. p 89-95.

Butler, R.W. 1977. Personal communication.

Campos, M.S, Wilcox, C.J., Becerril, C.M. and Diz, A. 1994. Genetic parameters for yield and reproductive traits of Holstein and Jersey cattle in Florida. J. Dairy Sci. 77: 867-873.

Darwash, A.O., Lamming, G.E. and Woolliams, A.J. 1997a. Estimation of genetic variation in the interval from calving to postpartum ovulation of dairy cows. J. Dairy Sci. 80:1227-1234.

Darwash, A.O., Lamming, G.E. and Woolliams, A.J. 1997b. The phenotypic association between the interval to postpartum ovulation and traditional measures of fertility in dairy cattle. Animal Science 65: 9-16.

Darwash, A.O. Lamming, G.E. 1997c. Abnormal ovarian patterns as a cause of subfertility in dairy cattle: protocols for early detection and treatment. Cattle Practice Vol. 5, Part 1: 3-7.

Darwash, A.O. Lamming, G.E. 1996 . The importance of progesterone levels during early pregnancy in the cow: Nottingham Cattle Fertility Conference. p 1-4.

Foote, R.H. 1996. A review: Dairy cattle reproductive physiology and management-past progress and future prospects. J. Dairy Sci. 79:980-990.

Hansen, L.B., Freeman A.E. and Berger, P.J. 1983. Yield and fertility relationships in dairy cattle. J. Dairy Sci. 66:293-305.

Harrison, R.O., Ford, S.P., Young J.W., Conely, A.J. and Freeman, A.E. 1990. Increased production versus reproduction and energy balance in high producing dairy cows. J. Dairy Sci. 62:1922-1931

Hayes, J.F.R., Cue, R. I. and Monardes, H.G. 1992. Estimates of repeatability of reproductive measures in Canadian Holsteins. J. Dairy Sci. 75:1701-1706.

Hermas, S.A., Young, C.W. and Rust, J.W. 1987. Genetic relationships and additive genetic variation in productive and reproductive traits in Guernsey cattle. J. Dairy Sci. 70: 1252-1257

Lamming, G.E. and Darwash, A.O. 1995. Effects of inter-luteal interval on subsequent luteal phase length and fertility in postpartum dairy cows. Biology of Reproduction 52:(suppl.1) 72 (abstr).

Marti, C.F. and Funk, D.A. 1994. Relationship between production and days open at different levels of herd production. J. Dairy Sci. 77:1682-1690

Nieuwhof, G.J., Powel, R.L and Norman, H.D. 1989. Ages at calving and calving interval in cattle in the United States. J. Dairy Sci. 72:685-692.

Oltenacu, P.A., Frick A. And Lindhe, B. 1991. Relationship of fertility to milk yield in Swedish cattle. J. Dairy Sci. 74:264-268.

Philipson, J. 1981. Genetic aspects of female fertility in dairy cattle. Livestock Prod. Sci. 8:307

Robertson, A. 1959. Experimental design in the evaluation of genetic parameters.

Biometrics, 469-485.

Seykora, A.J. and McDaniel, B.T. 1983. Heritability and correlations of lactation yield and fertility for Holsteins. J. Dairy Sci. 66:1486-1493

Swalve, H.H. 1995. The effects of test-day model on the estimation of genetic

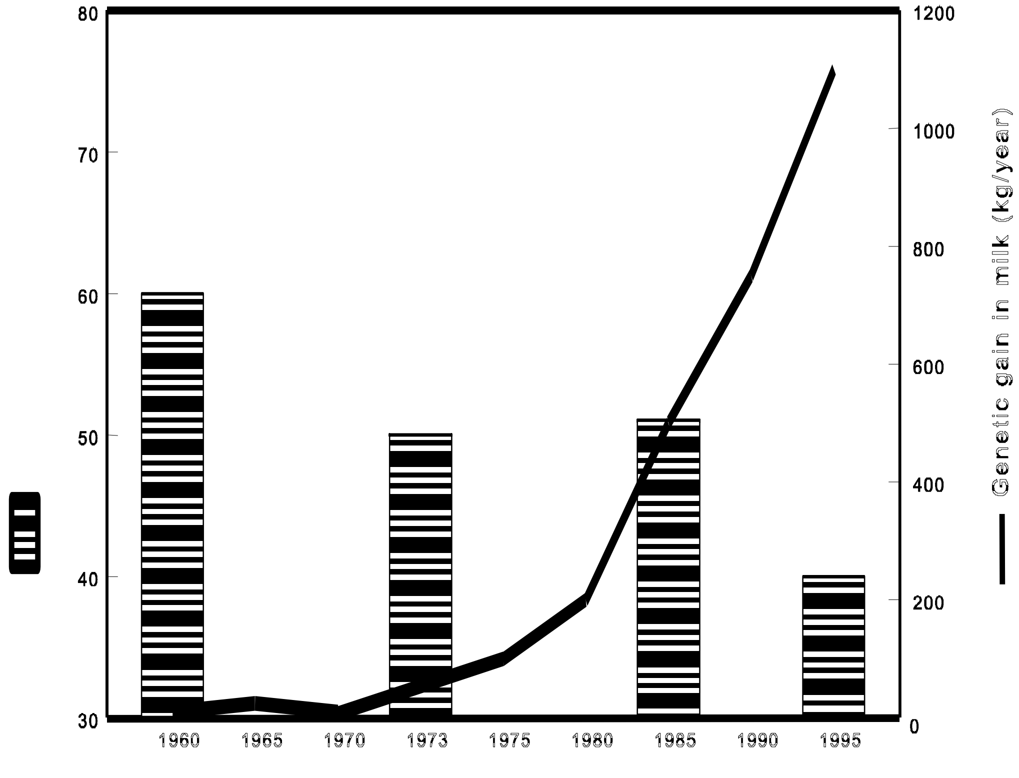
Woolliams, J.A. 1997. Trait selection and its importance in the genetic improvement of fertility in dairy cattle.

parameters and breeding values for dairy traits. J. Dairy Sci. 78:929-938.

Swiger, L.A., W.R. Harvey, D.O. Everson and Gregory, K.E.. 1964. The variance of intraclass correlation involving groups with one observation. Biometrics 20: 818-826.

Proc. Brit. Soc. Animal Science: p141(Abstract)

Fig. 1 Milk yield and conception rate in Holstein-Friesian cows



Milk data from Foote, R.H. 1996, data on conception rates from Butler, & Smith, 1989; Butler *et al* ., 1995 and Butler, 1997.

Fig. 2: Reproductive Parameters Studied

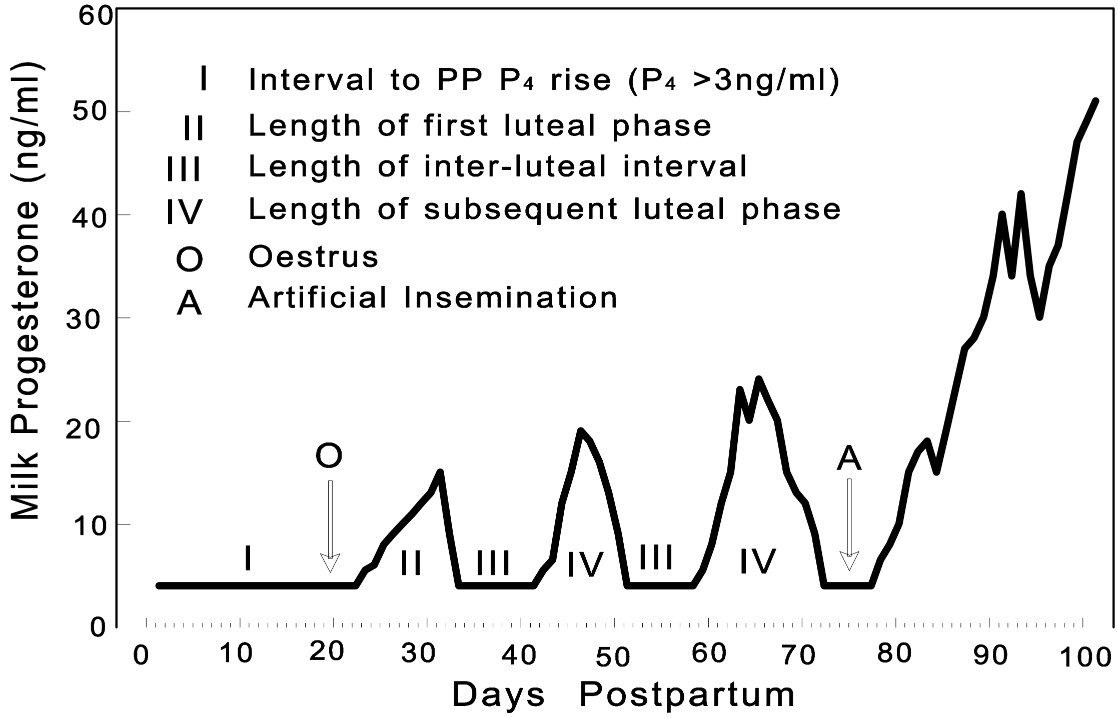
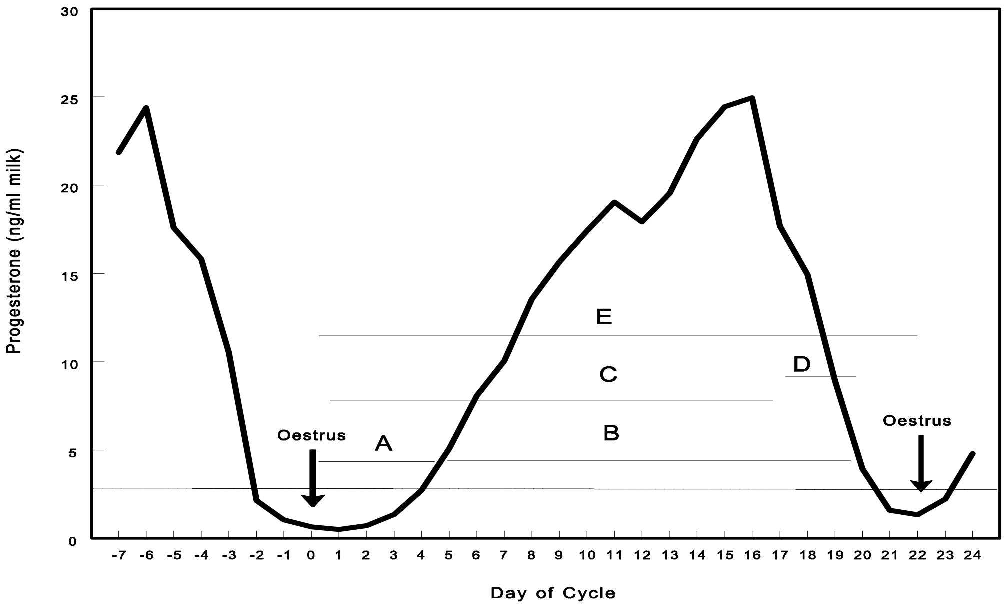


Fig. 3 Luteal phase parameters monitored using milk progestrone



A Oestrus to P4 riseB Luteal phase lengthC Oestrus to peak P4 levelD Peak P4 to CL demise E Inter-oestrual interval