Studies on fertility in dairy cattle, based on analysis of AI data

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STUDIES ON FERTILITY IN DAIRY CATTLE BASED ON ANALYSIS OF AI DATA

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C.C. Oosterlee,
in het openbaar te verdedigen
op vrijdag 21 november 1986
des namiddags te vier uur in de aula
van de Landbouwuniversiteit te Wageningen.

STELLINGEN

1. Bij de evaluatie van inseminatieresultaten van stieren dient rekening gehouden te worden met het effect van seizoen, bedrijf en de pariteit van het geïnsemineerde rund.

Dit proefschrift.

2. Het verband tussen de inseminatieresultaten van de stier en die van zijn dochters verandert met de leeftijd van de dochters.

Dit proefschrift.

3. Bij de huidige omvang van dochtergroepen van proefstieren in Nederland is fokwaardeschatting voor vruchtbaarheid bij melkkoeien niet zinvol.

Dit proefschrift.

4. De vruchtbaarheidssituatie op melkveebedrijven kan voldoende gekenschetst worden door de oestrusindex, eventueel aangevuld met de kengetallen het interval afkalven tot eerste inseminatie en het percentage niet-terug 56 dagen na eerste inseminatie.

Dit proefschrift.

5. Bestrijding van enkelvoudig recessieve gebreken wordt slechts van belang, indien de frequentie van het recessieve gen boven de één procent komt.

Jansen, J., Van Laarhoven, A. en Brascamp, E.W., 1984. Z. Tierzüchtg. Züchtgsbiol., 101: 220-228.

6. De beoordeling van benen en klauwen heeft ook in het nieuwe NRS-keuringsrapport geen poot om op te staan.

Smit, H., Verbeek, B., Peterse, D.J., Jansen, J., McDaniel, B.T. en Politiek, R.D., 1986. Livest. Prod. Sci., 15: 205-218.

7. Daar de huidige uitvalspercentages niet gecorrigeerd zijn voor steekproefeffekten zijn de onderlinge cijfers niet vergelijkbaar en levert de publikatie meer verwarring dan informatie op.

8. Identifikatie van nuchtere kalveren en uitbetaling aan de melkveehouder op basis van slachtwaarde zijn voorwaarden voor het voortbestaan van de vleeskalverensector op langere termijn.

9. De MRY-fokkerij bevindt zich momenteel in dezelfde fase als de friese in de zeventiger jaren.

10. De naam "Syndicaat" roept in het buitenland hetzelfde gevoel op als door NRS en FRS soms over en weer gekoesterd wordt.

11. De inseminator kan niet buiten de stier voor goede bevruchtingsresultaten.

Proefschrift van J.Jansen
Studies on fertility in dairy cattle based on analysis of AI data.
Wageningen, 21 november 1986.

aan mijn ouders

Jansen, J., 1986. Studies on fertility in dairy cattle, based on analysis of AI data (Onderzoek naar vruchtbaarheid bij melkvee of basis van analyse van KI-gegevens). Doctoral thesis, department of Animal Breeding, Agricultural University, Wageningen.

Voorwoord

Dit proefschrift bestaat uit een bundeling van vijf artikelen en een afsluitend discussiehoofdstuk. Het daaraan ten grondslag liggende onderzoek werd uitgevoerd toen de auteur als medewerker aan de vakgroep Veefokkerij van de Landbouwhogeschool verbonden was. Graag wil ik iedereen bedanken die bijgedragen heeft tot de tot standkoming van dit proefschrift. Enkelen wil ik met name noemen.

Allereerst mijn ouders, die mij gestimuleerd hebben tot een wetenschappelijke studie en de afronding daarvan middels dit proefschrift met belangstelling hebben gevolgd.

Mijn promotor prof.dr.ir. R.D. Politiek ben ik erkentelijk voor de ruimte die mij geboden werd in de vakgroep. Zijn voortvarendheid en vasthoudendheid heb ik zeer leren waarderen. Mijn co-promotor dr. Jan Dommerholt heeft mij geattendeerd op het onderwerp. Zijn kritische geest en ervaring hebben mede geleid tot een doelgerichte aanpak.

Zonder technische ondersteuning zou dit proefschrift niet tot een afronding zijn gekomen. Eppie Klein heeft een belangrijke bijdrage geleverd aan de opzet van de databank waaruit de gegevens voor het onderzoek geput werden. Gijs Lagerweij heeft het leeuwendeel van de voorbewerking en vooranalyses gedaan. Willem de Boer en Julius van der Werf hebben gezorgd voor de eindanalyses van het vierde artikel. Hun geduld is herhaaldelijk op de proef gesteld vanwege de beperkte computerfaciliteiten voor de analyse van gegevens van een dergelijke omvang. Van harte bedankt voor de plezierige samenwerking.

De soms pittige discussies in de leescommissie hebben geleid tot een duidelijke aanscherping van het onderzoek en de presentatie daarvan. Mijn vakgroepscollega's Siem Korver en Johan van Arendonk hebben ook daarbuiten veel belangstelling getoond voor de gang van zaken. De inbreng van buiten middels Aalt Dijkhuizen, Tette van der Lende en Rob Verdooren heeft tot duidelijke heterosiseffekten geleid. Ik denk met genoegen aan onze discussies terug.

Mevr. E. van Beek heeft het typewerk verzorgd, terwijl W. Heije de figuren getekend heeft. Mijn hartelijke dank daarvoor.

Het FRS heeft de nodige inspanningen verricht om de gegevens aan te leveren. Het LEB-fonds ben ik erkentelijk voor de financiële bijdrage tot de afronding van het proefschrift.

Contents

INTRODUCTION

Fertility is one of the non-yield traits which is of great economic importance in dairy herds. Reduced fertility results in prolonged calving intervals and in culling of cows with fertility problems. In Western Europe about 28% of all disposals are due to fertility problems (Dijkhuizen, 1980; Drees, 1982).

Artificial insemination (A.I.) was initially set up to reduce the incidence of veneral diseases, spread via natural service. In the early years of A.I. much attention was also paid to the elimination of specific fertility disorders with a genetic background (cystic ovaries, gonodal hypoplasia, impotentia coeundi).

Initially genetic analyses were mainly done on the basis of daughter-dam regression. A.I., however, provided a sound data structure to perform half-sib analyses, because offspring of sires can be distributed over many herds. This reduces the bias arising from environmental effects (especially herd effects).

Various studies showed that a small, but significant part of the variation in fertility traits derived from AI data, had a genetic background. These studies were reviewed in the first chapter, with emphasis on areas for further research. It was concluded that the following subject deserved further attention:

- The evaluation of male fertility and its relation with production
- genetic relationships between measures of fertility in cows in different parities
- genetic relationships between measures of fertility and milk production in early lactation.

Due to lack of data relationships of fertility and milk production could not be quantified. Instead the scope of the study was extended to management aspects in the analysis and evaluation of AI data.

Firstly the evaluation of non-return rates of bulls in A.I. was examined (chapter 2), of interest for the farmer when selecting bulls as well for the management of the AI stud. The evaluation of insemination results of technicians was included.

Secondly relationships between fertility of bulls and of their progeny were studied (chapter 3). In addition to parameters for the direct and indirect effect of the sire, also genetic parameters for the direct genetic effect (the embryo) and the maternal effect (the environment for the embryo) were quantified.

Thirdly genetic relations between fertility traits of cows in different parities were quantified (chapter 4). The methodology used in this study considered also the possible effect of selection for fertility. The production capacity of the cow is usually taken into account, when cows are culled for fertility (Van Arendonk, 1985).

In addition to the use of A.I. information for the genetic evaluation of fertility of bulls and progeny groups, and the evaluation of insemination results of technicians, A.I. information can also be used for herd management purposes. Therefore a study was conducted to derive parameters to monitor dairy herd fertility. Fertility variables calculated on the basis of A.I.-data, were related to financial losses from prolonged calving and culling due to fertility problems at herd level. These results are reported in chapter 5.

An integrated discussion of results of the studies mentioned and from recently reported studies by others is presented in the final chapter.

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Chapter 1

GENETIC ASPECTS OF FERTILITY IN DAIRY CATTLE BASED ON ANALYSIS OF A.I. DATA - A REVIEW WITH EMPHASIS ON AREAS FOR FURTHER RESEARCH

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Abstract

Recent research on genetic aspects of fertility in dairy cattle is discussed with emphasis on areas for further research. Field date (A.I.) are required to obtain reliable genetic parameters. Measures of female fertility should include both measures to assess prolonged calving intervals and measures for culling due to fertility problems. Genetic relationships between measures of fertility in virgin heifers and primipari were inconclusive, those between primipari and multiparae were unknown. Further research is needed in order to define breeding goal and selection index more precisely. Relationships between female fertility and milk production were varying, but an antogonistic relation prevailed. It needs further study to determine whether this is due to increased energy deficiency post partum and/or metabolic disorders. The relationship between measures of fertility and the course of fat and protein content and its ratio in early lactation needs further attention.

Male fertility has received less attention than female fertility. More effort should be directed to obtaining unbiased genetic parameters as well as to determining the relationship of male fertility to milk production and female fertility.

1. Introduction

Fertility is one of the non-yield traits which is of great economic importance in dairy herds. Reduced fertility results in prolonged calving intervals and in culling due to fertility problems. Fertility problems account for about 28% of all disposals in Western Europe (Dijkhuizen, 1980; Philipsson, 1981; Drees, 1982). In the USA the figure is about 16% (Freeman, 1983).

The economic consequences of reduced fertility have been studied several times. The calculation of economic losses had mostly been restricted to a prolonged calving interval (Louca and Legates, 1968; Zeddies, 1977; Olds et al., 1979). Calving intervals of 13 months for primiparae and 12 months for multiparae were reported to be optimum.

In a recent study Dijkhuizen (1983) considered both economic losses of prolonged calving intervals and forced replacement due to fertility problems under Dutch conditions. The total loss was Dfl. 80 per cow per year on average. Culling for fertility problems accounted for Dfl. 27.50 of the total loss, a prolonged calving interval for Dfl. 37.50. The loss of a prolonged calving interval was mainly due to reduced net milk returns per unit of time. Remaining factors contributing to the economic loss were reduced returns from calves born, insemination and labour costs. The computed total loss in other studies was mostly higher, because compensatory factors were neglected.

In this paper genetic aspects of fertility in dairy cattle will be discussed. As there have been many reviews in recent years (Maijala, 1976, 1978; Philipsson, 1981; Syrstad, 1981; Smidt and Farries, 1982; Freeman, 1983) it is not intended to repeat this. Rather we will focus on areas for further research using data obtainable via A.I. and milk recording. Dystocia will not be covered, as this was reviewed recently by Meijering (1984). Viability will not be dealt with either.

In this paper definition of traits and correction for environmental effects will be discussed first. Secondly attention will be paid to female fertility and its relation with production and finally male fertility and its relations with female fertility and production will be considered.

2. Definition of traits

Fertility can be measured in several ways. It is useful to distinguish among traits which are affected by the cow (female fertility), traits which are affected by the sire mated to the cow (male fertility) and traits which are affected by both. Male fertility may be called the direct effect of the sire, and female fertility the indirect effect of the sire. Traits like age at first breeding in heifers and the interval between calving and first oestrus or first insemination measure female fertility. Traits like volume, number of sperm and sperm quality measures, important in A.I., measure male fertility. Traits measuring the results of an insemination and reflecting conception rate are influenced by both male and female fertility. They include among others non-return rate, number of inseminations per conception or service period, conception rate, days open, calving interval and interval between services. As a conceptual framework measures of fertility can also be distinquished among (1) conceived or not and (2) length of time required for conception.

Field data are required to obtain parameters for the population of interest with a sufficient accuracy. Interpreting results from field data presents some problems, not only with respect to the relationship between fertility and production, as pointed out by Philipsson (1981), but also for fertility measures on their own. This applies to both male and female fertility.

If farmers were to have high producing cows inseminated later than low producing cows, genetic variation for the interval (calving) to first breeding would be inflated. Additionally, the measures days open, calving interval and to some extent conception rate do not include cows that are culled for fertility problems and cows that are kept open on purpose. The culling decision and time of disposal are economic decisions: a cow is culled because the farmer expects more from a replacement animal (Dijkhuizen, 1983). Dijkhuizen showed that high producing cows may be given more opportunities to conceive. It is not unlikely that this happens in reality.

Evaluation of male fertility on the basis of A.I. data also causes problems due to variations in semen processing which tend to minimize differences in conception rates among bulls.

It can be concluded that many measures of fertility reflect biological traits as well as actions taken for economical or other reasons. Therefore attention should be paid to both measures of fertility to assess prolonged calving intervals and measures of culling due to fertility problems.

3. Female fertility and correction for environmental effects

The statistical analysis of fertility traits presents some problems due to the categorical or non-normal nature of the traits. Meijering (1984) reviewed these problems for dystocia and stillbirth and therefore the statistical methodology as such will not be discussed further. References of interest can be found in his paper.

It is necessary to correct for effects of non-genetic origin to obtain unbiased parameters. The following effects were shown to be of interest: herd-year-season, parity, region (A.I.-stud) and technician (Janson, 1980; Distl, 1982; Drees, 1982; Haussmann and Kieninger, 1982; Hansen et al., 1983a).

The outcome of an insemination is usually not corrected for the bull used. This may be due to lack of information, computational problems or the small amount of variance explained by the mating bull. Haussmann and Kieninger (1982), however, reported that the variance component of the mating bull was higher than the female component. Besides, it is not likely that bulls are randomly distributed across herds with current A.I. programmes. The size of the bias is unknown. Regression of fertility measures on the mating bull or the herd were used as alternatives (Janson, 1980; Drees, 1982), but this may underestimate the genetic variance.

There is some indication of a sire by herd-year-season interaction. Berger et al. (1981) reported the interaction component to be higher than the sire component for the interval to first breeding. This was confirmed by Hansen et al. (1983a). Interaction effects on insemination results were absent (Berger et al., 1981) or smaller (Hansen et al., 1983a). The consequences of interaction on the ranking of sires need further study.

In some studies insemination results are corrected for the interval from calving to first breeding (Kräusslich et al., 1977; Gasteiger and Kräusslich, 1981). It is known that conception rates are improved at a decreasing rate if the interval to first breeding is extended (Berger et al., 1981; Esslemont, 1982). It is justified to correct for differences in interval to first breeding, if male fertility is studied and if no assortative mating is applied. When female fertility is studied, it can be argued that farmers postpone breeding of high yielding cows on purpose. In general this kind of preferential treatment within herd-year-seasons cannot be detected statistically.

Laben et al. (1982) found in Californian data that in herds where the farmer indicated some preferential treatment, a slightly longer interval to first breeding (2.4 days) was obtained and less inseminations (0.091) were required. They further indicated that high-producing herds started to inseminate earlier and did not require more inseminations. The regression of interval to first insemination on 180-day fat-corrected milk yield, however, tended to increase with level of production when the analysis was done within herd-production classes. Similar results were reported by Drees (1982). He found that the effect of short intervals to first insemination on conception rate after first insemination was more disadvantageous for high-producing cows than for low ones. Differences were small after 80 days. Furthermore it is reported that the anoestrus period varied widely (Baker, 1956; Claus et al., 1982) and that many cows exceeded the period required for an optimum calving interval before first oestrus was shown. It is concluded from these studies that there are biological differences between cows in the interval from calving to first breeding and that a correction of insemination results for interval to first breeding removes part of the variation, when female fertility is studied.

4. Genetic parameters of female fertility

Heritability estimates of fertility measures were low, generally below 5% (reviews by Maijala, 1976, 1978; Philipsson, 1981; Vinson, 1982). Heritabilities of days open were found to be slightly higher. There is, however, considerable genetic variation in measures of fertility, about 10% of the respective means. Although Hahn (1969) suggested that heritability may be best observed under stressful conditions, Drees (1982) did not detect clear differences between 100-day production classes. The question in this respect remains how to define stress. Milk production is probably only a minor indication of such conditions. A higher production is largely obtained by better management, causing an overall positive relationship between fertility and production, because well managed herds have better fertility.

Measures reflecting the outcome of an insemination within parities are highly correlated (0.6-1) (Janson, 1980; Berger et al., 1981; Drees, 1982; Hansen et al., 1983b). The genetic correlations between days open-interval to first breeding and days open-number of services were about equal (Table I) within studies and varied from 0.45 to 1.06 between studies. The genetic relation between interval to first

Table 1. Genetic correlation between interval to first breeding (FB), days open (DO) and number of inseminations per period (NS)

Author	Breed and parity	No. of records	FB-NS $r_g \pm$ S.E.	FB-DO $r_g \pm$ S.E.	DO-NS $r_g \pm$ S.E.
Janson (1980)*	Swedish Red and White cows (all parities)	14386	- 0.07 ± 0.32	0.48 ± 0.32	0.78 ± 0.20
Berger et al. (1981)	Holstein Friesian (1)	16808	0.27 ± 0.30	0.79 ± 0.17	0.73 ± 0.18
	Holstein Friesian (2)	15209	0.09 ± 0.38	0.54 ± 0.22	0.45 ± 0.27
	Holstein Friesian (> 3)	30129	0.38 ± 0.13	0.75 ± 0.09	0.86 ± 0.04
Hansen et al. (1983b)**	Holstein Friesian (1)	41710	0.45 ± 0.16	0.84 ± 0.16	0.68 ± 0.10
	Holstein Friesian (2)	31162	0.78 ± 0.36	0.87 ± 0.12	1.06 ± 0.17
	Holstein Friesian (3)	22389	0.53 ± 0.10	0.96 ± 0.10	0.51 ± 0.33
Drees (1982)	German Friesian (1) Red and White HF-crosses	13131	0.10	0.93	0.88

* Instead of NS - number of services per calving; DO - calving interval.

** A maximum of three services and 150 days open allowed to circumvent preferential treatment.

breeding and number of services seems to be positive as well, except for Janson's results (1980). In the data of Drees (1982) the phenotypic relation was slightly negative (-0.12), but the genetic correlation was positive (0.10). This indicates that even if farmers try to inseminate high-producing cows later, a positive genetic correlation between interval to first breeding and number of services exists. Results of the work of Hansen et al. (1983b) showed the highest relation between interval to first breeding and number of services in second parities. Whether this was due to the high interaction component between herd-year-season and sires is not clear.

Repeatabilities of measures of fertility were generally less than 0.10, except for interval to first breeding and days open which may be as high as 0.16 (Hansen et al., 1983a). Low repeatabilities may suggest a low heritability, but also a low genetic correlation. To our knowledge no studies are available with respect to the genetic relationships between fertility measures in different parities. Understanding of these relationships is necessary for the definition of the breeding goal for fertility. Additionally it can illuminate differences found with respect to the relation between yield and fertility in different parities (Hansen et al., 1983b). Preliminary results (Van de Broek and De Jager, 1983) suggest that the relation between days open in first and second lactation is quite low (-0.07).

To obtain a sufficiently accurate sire evaluation it would be useful if data of virgin heifers and first calvers could be used. Janson (1980) found in Swedish Red and Whites that non-return rate (56 days) as well as number of inseminations per service period were highly correlated in virgin heifers and first calvers (r_g = 0.6-1.0). Hansen et al. (1983c) obtained much lower values (0.1-0.3) in Holsteins, while Distl (1982) found values of 0.88 and 0.55 in Simmental cattle. Is is not clear whether this difference is due to breed effects, statistical methods used or to other reasons.

The relationship between fertility measures determining days open and culling due to fertility problems is difficult to study in field data. Culling for fertility problems increased with age (Dijkhuizen, 1980). Dijkhuizen (1983) found that differences in losses due to fertility problems between herds were more determined by differences in rates of culling than by differences in calving interval, as culling accounted for 71% of the variance between herds. The cost of a prolonged calving interval on a herd basis was slightly negatively correlated with the cost due to culling. Miller et al. (1967) reported that calving interval and herd life were genetically correlated (0.3). Further research is needed in this area. This should include the relationship between fertility measures and culling. Definition of all-or-none traits like pregnant at day 85 post partum or non-return rate within 28 days at 115 days post partum could be useful in this respect.

5. Relationship of female fertility and production

The relation of fertility and production has been a major concern. An indication of a negative relationship between fertility and production is provided by a comparison of Holstein Friesians and other Black and White strains, all originating from the same base population in The Netherlands. Holsteins have been selected more strongly for milk production but a negatively correlated response for fertility is observed, both with respect to conception rates and culling for fertility problems (Lederer, 1978; Oldenbroek, 1984). Designed selection experiments for milk production, however, did not show any negative response on fertility traits (Shanks et al., 1978; Hansen et al., 1979). It is unclear whether this is due to the short period of the experiments or better management which could mask minor differences as discussed before. Genetic correlations from field data were summarized by Philipsson (1981). Although results were ambiguous, an antagonistic relation prevailed. Results from Hansen et al. (1983b) supported this. Berger et al. (1981) and Hansen et al. (1983b) reported different relationships within paraties, especially in early lactation. Peak production was positively related to interval to first breeding, number of services and days open in first and second lactation, but negatively related in third lactation. Relationships with 305-day yield changed from slightly positive to zero. This could reflect a genetic difference between parities but could also be a result of selection within a generation or sampling (Freeman, personal communication, 1984).

Furthermore carry-over effects of fertility in the previous lactation might be of interest. Funk (1983) looked at the combined phenotypic effect of previous days open, previous days dry and present days open on milk production. He concluded that these traits did not affect lactation yield differently by parity when all the effects were fitted simultaneously. It should be researched whether this is also valid genetically.

It has been argued that stress due to production and a negative energy balance in early lactation are responsible for reduced fertility. A negative energy belance could be approached through changes in live weight. Broster (1973) in a review could not draw any definite conclusions from the relationship between weight, weight change and fertility measures. Also no genetic parameters were given. It should be mentioned that live weight changes are a rather inaccurate method by which to assess changes in energy metabolism (Korver, 1982). Besides weight the protein content of the milk can be used for energy status. Korver (1982) found that distinct underfeeding reduced the protein content of the milk. In addition, the protein content was not correlated to the fat content in the period of underfeeding, while values of about 0.5 were found on a lactational basis (review Maijala and Hanna, 1974). Grieve (personal communication, 1984) found that the ratio of fat to protein content explained a significant proportion of the difference between energy intake and energy output after fitting breed, parity and feeding regime.

Hansen et al. (1983a) found no effect of parity on measures of fertility. Drees (1982), however, found that primiparae had longer intervals to first breeding and lower conception rates than multiparae, resulting in longer calving intervals for primiparae. This can partly be caused by a higher incidence of dystocia (review Meijering, 1984), but primiparae also produce milk with a lower protein content, indicating higher energy deficiency (-0.05, CMD, 1983).

Recently Reid (1982) has drawn attention to the relation between fatty livers and reduced fertility. Cows having a fatter liver at parturition took more time for the onset on first oestrus and had on average a 33-day longer calving interval than cows not affected. According to Farries (1983) fatty livers cause reduced feed intake post partum, thus increasing the energy deficiency. These metabolic disturbances increase the fat content of the milk, especially the long chain unsaturated fatty acids, and decrease the protein content.

Additionally cows having a fatty liver were more susceptible to mastitis, suggesting an association between fatty livers, fertility and disease resistance (Reid, 1982). This is probably less important in primiparae, because fatty livers were hardly found in heifers. It should be mentioned in this context that restricted feed intake ante partum reduces fatty liver problems and increases feed intake post partum (Farries, 1983). As fatty livers already start to develop a few weeks before calving, however (Reid, 1982) it can be concluded that energy deficiency as such is not the only cause of impaired fertility in multiparae. Differences in feeding ante partum could be responsible for the observed sire by herd-year-season interaction and inconclusive relationship between fertility and production/live-weight change.

As reliable genetic parameters for live weight (change) and metabolic disorders are hard to obtain from field data, the relationship between protein content, the ratio of protein to fat content in early lactation and fertility should be investigated in more detail.

6. Male fertility

In contrast to work on dystocia, most attention and research on fertility has been directed towards female fertility or the indirect effect of the sire.

Syrstad (1981) states that male fertility is as important as female fertility with respect to conception rate. In breeding programmes, however, selection for male fertility can be done earlier than selection for female fertility. This may be of less interest, as sires will not be used heavily until the results of progeny test for milk production are known. Nevertheless the direct effect of the sire, when progeny-tested, is expressed some years earlier than the indirect effect, causing the discounted value of male fertility to be higher than that of female fertility.

Non-return rate had mostly been used as a measure of male fertility. Most estimates of heritability have been based on annual non-return rates. These estimates are biased as no correction is done for the differences in distribution across seasons and for other non-genetic factors, as well as differences in female fertility. Heritability estimates of male fertility based on bulls used in active A.I. service may be biased downward by selection. The selection intensity on male fertility, however, is low and mostly not based on non-return rate itself. Therefore the effect of selection is probably small.

In his review Syrstad (1982) found heritability estimates ranging from 0.1 to 0.6. Estimates were not comparable because the number of inseminations per bull varied. Heritability estimates of non-return of a single insemination (60-90 days) were 0.015 or less (Hansen, 1979; Murray et al., 1978), suggesting less genetic variance in male than female fertility.

It has been argued (Vinson, 1982) that estimates should be based on randomly distributed semen from young bulls in order to avoid bias. Correlations between non-return rate of young bulls and non-return rates of the same bulls after progeny testing, however, were rather low (0.4; Murray et al., 1978; Syrstad, 1982). To what extent this could be due to differences in semen processing is unknown. Estimates based on inseminations from young bulls seem to have predictive value only if semen, used after progeny test, is frozen at a young age.

Genetic correlations between male and female non-return rates ranged from 0.3 to 0.4 (Hansen, 1979; Syrstad, 1982). Thus male fertility is rather inefficient in improving female fertility and vice versa. It should be investigated whether these correlations are age-dependent both on the male and female side.

There are only a few studies available with respect to the relationship between male fertility and milk production. Estimates by Murray et al. (1978) (-0.26) and Syrstad (1982) (-0.2) showed a small but significant negative relationship. From these figures no severe decline in male fertility can be expected, if proven bulls are solely selected for milk production. As proven bulls are very frequently used, however, male fertility should be evaluated too in order to avoid negative values in individual cases. These estimates should be corrected as much as possible for environmental effects and differences in numbers of inseminations.

7. Conclusions

Research on genetic aspects of fertility in dairy cattle based on analysis of A.I. data should focus on the following areas:

1. Genetic relationships between measures of female fertility in different parities. This should include both measures to assess prolonged calving intervals and measures for culling due to fertility problems;
2. Genetic relationships between measures of fertility and milk production traits in early lactation, especially the course of fat and protein content and its ratio;
3. Unbiased estimates of genetic parameters of measure of male fertility and its relation with milk production.

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Chapter 2

CORRECTION OF INSEMINATION RESULTS OF TECHNICIANS AND FRIESIAN BULLS IN A.I.

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Abstract

The correction of insemination results of technicians and Friesian bulls in AI was studied using 87112 first inseminations by 283 bulls and 37 technicians. The traits studied were 28 and 56 days non-return rates. Models were compared on the basis of the correlation between solutions obtained in a reference model and reduced models.

Age at first service in heifers and calving to first service interval in cows did not affect the ranking of sires and technicians. The routine monthly evaluation of non-return results of sires required a correction for parity of cow and month of insemination. In addition group of descendents and number of inseminations should be considered. The monthly evaluation of technicians can be based on deviations within studs.

An annual evaluation of sires and technicians should include a herd effect as well. The correlation between solutions (56 days non-return) in the full model and one without a herd effect was 0.94 for both sires and technicians, whereas the absolute average change was 0.5%.

1. Introduction

Artificial insemination studs in The Netherlands evaluate non-return rates of bulls and technicians on the basis of monthly averages of cumulative yearly averages. Results of technicians may be used for management purposes in AI-organisations. Results of bulls are frequently published together with information with respect to breeding values for production and management traits. In addition to the latter traits non-return rates may be taken into account when expected returns from an insemination are calculated (Everett, 1975; McMahon et al., 1985).

Besides differences due to bulls and technicians, differences in non-return rates are also caused by effects of herd-year-season, parity, genetic group and the interval calving to first service (Jansen, review, 1985; Taylor et al., 1985). These effects, however, are usually not taken into account in the evaluation of bulls and technicians. This may result in bias dependent on the confounding of these effects with bulls and technicians. Furthermore confounding of bulls and technicians may cause bias in the results.

The purpose of this investigation was to study whether the monthly and yearly evaluation of insemination results of bulls and technicians required a correction for the effect of year, month and herd of insemination and interval to first service and parity of cows.

2. Material

Breeding receipts were obtained from 326 herds with Friesian cattle from the province of Friesland. Data were provided by the Friesian Cattle Syndicate (FRS), spanning July 1, 1979 to February 29, 1984. Procedures for selection of the herds and a description of all the data collected are given in Kooper and Wilmink (1983).

AI data were matched by parity with registration and calving data. The criteria for validation of data and assignment of lactation numbers are given in Jansen (1986). After matching, the following records were removed: records with no insemination data or non-AI breedings, records with no exact sire of insemination or technician code, age at first service in heifers less than 338 or greater than 631 days and interval calving to first insemination less than 30 or greater than 155 days. Technicians were required to have at least 50 inseminations per parity. To provide equal opportunity for conception records with a first insemination past June 1983 were removed. Finally, bulls were required to have at least 55 inseminations in cows in order to get a manageable matrix. This reduced the number of sires from 683 to 283. Table 1 summarises the different editing steps.

Table 1. Editing of records in sequence of selection

	parity				
	0	1	2	3	≥ 4
initial number	52390	28977	23907	18517	33721
removed because of no inseminations	38388	1419	1023	636	1034
non-AI breedings	502	55	29	29	39
interval restriction[1]	461	773	510	397	749
no exact technician or bull code	4	93	396	314	657
< 50 ins. per inseminator	266	54	34	34	66
past June 1983	-	3342	2988	2456	4504
< 55 ins. per bull	1566	4507	1013	700	1362
remaining	11203	18734	17914	13951	25310

1 : interval to first insemination in heifers > 338 days and < 631 days
interval calving to first insemination > 30 days and < 155 days.

3. Methods

3.1. Models

The basic linear model considered the following effects:

- herds (326)
- genetic group. Two groups of bulls were considered. One group contained 100% Holstein bulls, either with imported semen or semen produced within the country. The other group comprised mainly 100% Dutch Friesian bulls but also a few crossbreds of Holsteins with Dutch Friesians.
- sire of insemination (283)
- technician (37)
- parity (0,1,2,3 and $\geq$ 4)
- year of insemination (4 years from July to June next year)
- month of insemination (12)
- age at first service in heifers and interval calving to first service in cows. The continuous variables age at first service and interval to first service were divided into classes according to table II.

The traits considered were 28 days and 56 days non-return rate after first insemination (NR28 and NR56).

Table II. Distribution of records according to classes for age at first service or interval to first service.

age at first service		interval to first service	
days	number	days	number
< 400	209	< 45	2604
400-419	712	45-50	3006
420-429	842	51-55	3748
430-439	1305	56-60	5305
440-449	1574	61-65	7490
450-459	1576	66-70	8267
460-469	1205	71-75	8088
470-479	881	76-80	7354
480-499	1192	81-85	6867
500-549	1147	86-90	5537
> 549	560	91-95	4120
		96-100	3181
		101-110	4384
		111-120	2566
		> 120	3392

Firstly ordinary least squares analyses per parity were carried out to study the effect of interval calving to first service/age at first service and the interaction year times month. In these analyses all effects except the herd effect were considered. Because the monthly pattern per parity seemed to differ, the interaction parity*month was subsequently tested in cows (parities 1,2,3 and greater than or equal 4) and in all data. In the latter case the effect of interval to first service and age at first service were not taken into account.

Finally evaluation procedures were compared using mixed models.
The following general model was applied:

$$\underline{y} = \underline{X}\underline{\beta} + \underline{Z}\underline{u} + \underline{e}$$

where

$\underline{y}$ = NR28 or NR56
$\underline{\beta}$ = vector with fixed effects
$\underline{u}$ = vector of sire effects
$\underline{e}$ = error,

$\underline{X}$ and $\underline{Z}$ are design matrices relating the fixed effects and the sire effect to the observations. $\underline{y}$, $\underline{u}$ and $\underline{e}$ were considered random with expectations and variances

$$E\begin{bmatrix}\underline{y}\\ \underline{u}\\ \underline{e}\end{bmatrix} = \begin{bmatrix}\underline{X}\underline{\beta}\\ \underline{0}\\ \underline{0}\end{bmatrix}$$

$$V\begin{bmatrix}\underline{y}\\ \underline{u}\\ \underline{e}\end{bmatrix} = \begin{bmatrix}\underline{Z}\underline{Z}'\sigma^2_u + \underline{I}\,\sigma^2_e\\ \underline{I}\,\sigma^2_u\\ \underline{I}\,\sigma^2_e\end{bmatrix}$$

Solutions for β and u were obtained from the normal equations

$$\begin{bmatrix}\underline{X}'\underline{X} & \underline{X}'\underline{Z}\\ \underline{Z}'\underline{X} & \underline{Z}'\underline{Z} + k\underline{I}\end{bmatrix}\begin{bmatrix}\underline{\beta}\\ \underline{u}\end{bmatrix} = \begin{bmatrix}\underline{X}'\underline{y}\\ \underline{Z}'\underline{y}\end{bmatrix}$$

In the normal equations a ratio k (σ^2_e / σ^2_u) of 350 was added to the sire*sire (Z'Z) part. This ratio corresponds to a heritability of about 1%. The make up of the fixed effects will be presented when the results are discussed.

3.2. Criteria for comparison

Dempfle and Haggar (1983) proposed the correlation between split samples as a criterion for comparison of models. The model with the highest correlation between split samples e.g. of sires or technicians, would be the best. The correlation between split samples, however, may be biased due to confounding of the effect considered and other effects in the model and was therefore not used. Instead the model with the smallest mean square error and all effects significant, was choosen as the reference model. Reduced models were subsequently compared on the basis of correlations.

4. Results and Discussion

4.1. Interval to first service

Average non-return rates by parity are given in table III. 28 days and 56 days non-return differed by about 8%.

Table III. Average non-return rates by parity

parity	NR28	NR56
0	83.44	77.01
1	79.69	71.64
2	78.80	70.51
3	78.07	69.56
≥ 4	76.01	67.11

First data of cows only were used to study the effect of interval to first service. All effects except the herd effect were considered. A correction for the interval to first insemination hardly affected the ranking of sires. The correlation between the solutions with and without a correction was 0.998 and 0.997 for NR26 and NR56, respectively. This is due to the fact that sires and interval calving to first service were rather balanced. Therefore the interval to first service could be dropped from the model in cows. Least squares constants for age at first service in heifers showed no clear pattern and this effect was therefore also not considered further. The latter is in agreement with Janson (1980) and Hansen et al. (1983). As the results for NR28 and NR56 were essentially the same, the comparison of models was restricted to NR56.

4.2. Monthly evaluation

The monthly evaluation of bulls and technicians within studs in The Netherlands is based on data of the last year up to the last month. A model containing a herd effect is not feasible due to the large computional efforts involved every month. Therefore the herd effect was left out when the monthly evaluation was studied in more detail. Correlations between sire solutions from different models are shown in table IV. Although the interaction between month and parity was significant, primarily due to a different pattern in heifers and to some extent older cows, hardly any differences in ranking were found compared to a model with month and parity separately (r=0.995). When parity, month and year were dropped, the correlation was reduced to 0.932. The largest change occurred when groups were subsequently removed from the model (r=0.791).

Table IV. Correlations between sire solutions from different models

	model			
model with fixed effects	2	3	4	5
1. group, technician, parity*month, year	0.995	0.932	0.791	0.735
2. group, technician parity, month, year		0.945	0.802	0.752
3. group, technician			0.851	0.731
4. technician				0.835
5. sire fixed				

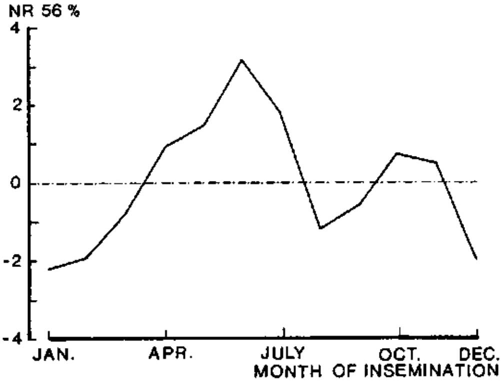

Fig. 1. Pattern of 56 days non-return rate over the year.

The pattern of NR56 over the year is shown in figure 1. The drop in August and September may be a result of reduced quality of heat detection due to the holiday season and reduced energy content of the roughage at the end of the grazing period. Poorest results were obtained in the winter season, when cows are kept indoors. Our results are rather similar to those of Janson (1980), but differ from Thibault et al. (1966), cited by Janson (1980) and McDaniel (personal communication, 1984). The seasonal pattern is clearly dependent on managemental and climatological conditions. Differences between years were rather small. As the monthly evaluation is done within years, the effect can be neglected.

Least squares constants for parities are shown in table V. Results for heifers may be biased upwards due to unknown use of natural service during the grazing period. Records with known natural service had been removed. First and second parity cows hardly differed, but third parity and especially older cows had clearly lower results. Our results differ from De Kruif (1975). He reported highest calving rates for four-year old cows, while two-year old cows had 7% lower calving rates than four-year olds.

Currently results of sires are presented as raw averages or deviations from the average, not accounted for sampling effects. Therefore a model with sires fixed was also included. As expected this affected the results greatly. The correlation was reduced to 0.735.

Table V. Least Square Constants by parity

parity	NR28	NR56
0	4.09	5.75
1	-0.12	-0.27
2	-0.14	-0.27
3	-0.86	-1.30
≥ 4	-2.98	-3.90

Table VI. Correlations between solutions for technicians from different models

	model		
model with fixed effects	2	3	4
1. group, technician, parity*month, year	0.999	0.994	0.987
2. group, technician parity, month, year		0.995	0.987
3. group, technician			0.991
4. technician			

Correlations between solutions for technicians from different models are given in table VI. In all cases correlations were larger than 0.985. It can be concluded that the evaluation of technicians does not require any correction, primarily because of a more balanced distribution across these effects. These results differ from those of Chavaz and Weber (1985), who proposed to correct results of technicians for parity, bull and month of insemination. Despite continuous guidance considerable differences between technicians were found. The range in solutions was about 9%.

Both for sires and technicians rather large numbers should be considered before sufficiently repeatable conclusions can be drawn from the monthly evaluation. For sires 300 first inseminations were required to obtain a repeatability of about 50% (cf. Solbu, 1972). At least 200 first inseminations are needed for technicians to obtain standard errors less than 3%.

4.3. Annual evaluation

Subsequently models for the annual evaluation were studied. The reference model contained the following fixed effects: herds, group, technician, parity*month and year. Figure 2 gives the distribution of estimated breeding values for NR56. The distribution was slightly skewed to the left, primarily due to one outlier.

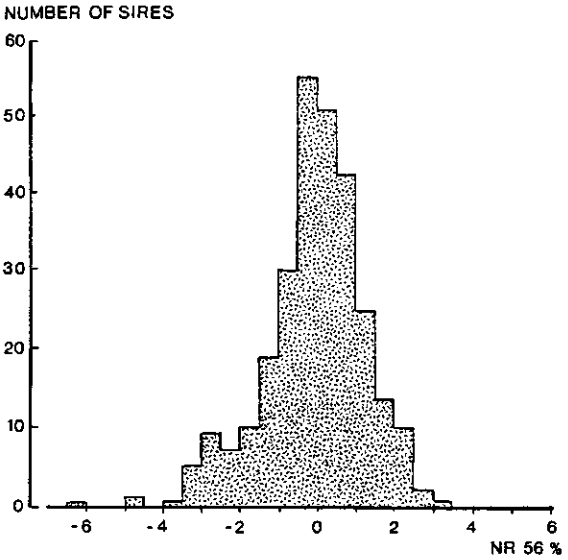

Fig. 2. The distribution of sire effects for 56 days non-return rate.

Table VII. Comparison of solutions for sires from reduced models and a model with effects of herd, group, sire, technician, year and parity*month

fixed effects in reduced model	correlation	average absolute change	average of 10 largest abs. changes
1. group, technician parity*month, year	0.944	0.05	1.44
2. group, technician parity, month, year	0.935	0.06	1.48
3. group, technician	0.894	1.01	3.50
4. technician	0.825	0.64	3.29
5. sire treated fixed	0.793	3.75	12.09

Table VII shows the results of the comparison of the different reduced models with the reference model. In addition to the correlation the average absolute change and average of ten largest absolute changes were calculated. Omitting the herd effect had a considerable effect; the correlation between the solutions of the two models was 0.94. The average absolute change was about 0.5%, whereas the average of the 10 largest changes was 1.44%. When the interaction parity*month was neglected subsequently, the results were about equal (r=0.935). When parity, month and year were left out of the model, the correlation was further reduced to 0.85. The lowest correlation was found when sires only were considered in the model and treated as being fixed. Then the correlation dropped to 0.79. The average absolute change was 3.75% and the average of the 10 largest changes was 12.1%.

From these results it is concluded that a herd effect should be included in the model for an annual evaluation of 28 and 56 days non-return rates of sires, as well as the effects of group, parity*month and year. The effect of technician could be left out as there was not much confounding between sires and technicians.

A stud effect could not be considered, because data of one stud only were available. Differences between studs may be due to differences between areas in which the studs operate. Inclusion of the herd effect in the model takes account for differences in non-return rate between different areas. Another cause of differences between studs may be differences in semen processing. These differences, however, affect the results of bulls and should therefore be maintained.

The comparison of solutions for technicians in the reference model with a herd effect and a model without, gave similar results as for sires. Dependent on the correction for parity, month and year the correlation ranged between 0.91 and 0.94. The absolute average changes varied from 0.55 to 0.66%.

Analysis of NR56 will be sufficient for the annual evaluation. The monthly evaluation of sires and technicians may include NR28 in order to be more up to date.

4.4. Conclusions

From these results it is concluded that routine evaluation of sires for non-return rates can greatly be improved by a correction for group of descendance, parity and month of insemination. Subsequently deviations from the average have to be regressed to account for sampling effects. For an annual evaluation the herd effect should also be considered. Despite the low heritability, still considerable differences in non-return rates between sires can be found. In our study the range was 10%. The monthly evaluation of technicians can be done on the basis of deviations within studs. In an annual evaluation this can be improved by accounting for the herd effect.

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Chapter 3

DIRECT AND MATERNAL GENETIC PARAMETERS OF FERTILITY TRAITS IN FRIESIAN CATTLE

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Abstract

Variance and covariance components for sire of cow and sire of insemination of fertility traits were estimated by parity using REML-procedures. Subsequently direct genetic and maternal components were calculated. Heritabilities for 56 days non-return rate, conception rate (heifers, parity one to three) and days open (parity one to three) varied between 0.007 and 0.049. The heritability for age at conception in heifers was 0.192. The maternal component for days open was greater than the direct genetic component. The genetic correlations between sire of insemination and sire of cow for non-return rate changed from -0.29 in heifers to 0.59 in parity three, that for conception rate from -0.74 to 0.48. The relation between maternal and direct genetic components changed from -0.94 to 0.26 and -0.97 to 0.12 for non-return and conception rates respectively. Changes in correlations for days open from parity one to three were smaller. The results indicated that the genetic correlation between the sire of cow components for non-return and conception rate in heifers, first parity and older cows may differ from unity.

1. Introduction

The outcome of an insemination is influenced by both the sire of insemination and by the cow. The cow provides the uterine environment and influences the quality of the egg (maternal effects), and has also a direct genetic effect on the embryo. The sire has an effect via the quality of the sperm and the genes transmitted to the embryo (direct effect). Indirectly, the sire affects the fertility of the cow one generation later via genes transmitted to the cow.

Information concerning the relation between the direct and indirect effects of the sire on fertility is limited. Hansen (1979) and Syrstad (1982) reported genetic correlations of 0.3 to 0.4 between non-return rates of the sire and those of his female progeny. It is unknown whether this relationship is dependent on the age of the sire and of his progeny group.

The direct and the indirect effects of the sire on fertility have hardly been studied simultaneously. Haussmann and Kieninger (1982) reported that the direct component of variance for the trait "interval between first and last insemination" was greater than the indirect component (0.64% to 0.36% of the total variance). In this study the interval between calving and first insemination was used as a covariable and therefore the indirect sire component may be reduced (Jansen, 1985).

Because the sire of insemination and the sire of the cow both transmit genes to the embryo, these components will be related per se. This relation depends on the size of the maternal component and the correlation between the maternal and the direct genetic component. Both are unknown. This information is, however, of interest to predict the possible effects of selection on fertility of sires for the fertility of their progeny and vice versa.

The purpose of this study was to estimate the direct and indirect sire components of variance on fertility and their covariance as well as the underlying direct genetic and maternal components. The analysis was within parity to study the effect of age of the cow on the parameters.

2. Material

Breeding receipts were obtained from 326 herds with Friesian Cattle from the province of Friesland. Data were provided by the Friesian Cattle Syndicate (FRS), spanning July 1, 1979 to February 29, 1984. These herds had been selected to establish a data base for research on field data. The procedure for selection of the herds and a description of all the data collected, is given by Kooper and Wilmink (1983).

Insemination data were matched with registration and milk recording data. The basic data sets contained 57812 registration records, 126476 lactation records and 210296 insemination records. Reasons for removing cows or records from the data base were: cows not registered, age at first calving less than 631 days, calving before June 10, 1979, lactation lengths greater than calving intervals and intervals between subsequent inseminations longer than 300 days.

Because lactation numbers were not available, lactation numbers for the first available record were assigned according to table I. Later lactations were numbered consecutively. Only records of parities 0 (heifers), 1, 2 and 3 were used for further analysis. To provide equal opportunity for conception, records with the last insemination after March 31, 1983 were removed.

Table I. Lactation number of first available record according to age at calving (days) and total number of records by parity

parity	age at calving	total number
0	-	52390
1	631 - 990	28977
2	1021 - 1260	23907
3	1381 - 1620	18517
≥ 4	> 1771	36910

Records were only used if the calving date of the subsequent lactation was known. The following selection criteria were used after inspection of the raw data. Age at first insemination in heifers was restricted to at least 338 days, but less than 631 days; the interval between calving and first insemination to 30 and 155 days; gestation length to 263 and 293 days in heifers and 264 and 294 days in cows. Subsequently animals were removed if they had been inseminated by an inseminator with less than 50 inseminations per parity. This was done after some confounding between sire of insemination and inseminator had been detected. Finally animals with an unknown sire were removed.

Table II. Editing of records in sequence of selection

	parity			
	0	1	2	3
starting	52390	28977	23907	18517
subsequent calving date > 990 days	10164	-	-	-
no inseminations	23664	1419	1023	636
no exact insem. data	421	1	-	-
inseminations past March 31, 1983	4876	5893	5006	4046
gestation length	1733	1320	943	677
age/interval to first service	328	574	362	289
inseminator < 50 insem.	70	257	167	159
unknown sire	960	4819	4577	3830
culled during lactation	1202	1986	1767	1581
remaining	8972	12708	10062	7299

The editing steps for parities 0, 1, 2 and 3 aresummarized in table II. The main causes for loss of records were: no insemination data (26742 records), age restrictions on young heifers (10164), time restrictions (19821) and no sire identification (14186). The number of records remaining were 8972, 12708, 10062 and 7299 records for parities 0, 1, 2 and 3 respectively. The number of sires was too large to calculate the inverse of the design matrix (672, 1257, 128 and 1050 sires in parity 0, 1, 2 and 3 respectively). Therefore a minimum was imposed on the number of herds in which sires should have daughters or inseminations. In this way the effects of a possible confounding of herds and sires were also reduced. The limits, the number of sires meeting the limits and the total number of records remaining are given in table III. As a rule first lactation heifers have to be inseminated with unproven sires in The Netherlands and therefore many sires had no daughters and only a small number of inseminations in first parity. The total number of sires which were evaluated, was 84, 125, 115 and 96 for parity 0, 1, 2 and 3, respectively.

Table III. Minimum number of herds in which sires had either progeny, inseminations or both (number of remaining sires in brackets)

parity	sire of cow	sire of insemination	both	records left
0	12 (11)	12 (6)	8 (67)	6497 (84)
1	25 (12)	55 (48)	25 (65)	3704 (125)
2	20 (16)	20 (20)	10 (79)	6883 (115)
3	20 (17)	20 (19)	10 (60)	4711 (96)

3. Methods

3.1. The genetic model

The genetic model for a trait which is influenced by both the sire of the cow and the sire of insemination is described by Wilham (1963) and Van Vleck (1978). When we ignore all other fixed and random effects, the result of an insemination can be described by

$$p = s_i + t_j + e$$

where p = result of an insemination
s = sire i of cow (indirect sire effect)
t = sire j of insemination (direct sire effect)
e = error

Then $\sigma^2_p = \sigma^2_s + \sigma^2_t + \sigma^2_e$

Now s_i contains half of the maternal effect (m) and 25% of the direct genetic effect (d), whereas t_j contains half of the direct genetic effect.

$$s_i = 1/4\ d_i + 1/2\ m_i$$

$$t_j = 1/2\ d_j$$

The variance and covariance components for the direct and indirect are then composed as follows

$$\sigma^2_s = 1/16\ \sigma^2_d + 1/4\ \sigma^2_m + 1/4\ \sigma_{dm}$$

$$\sigma^2_t = 1/4\ \sigma^2_d$$

and $$\sigma_{mt} = 1/8\ \sigma^2_d + 1/4\ \sigma_{dm}$$

Thus the direct genetic and maternal components can be calculated after the variance and covariance components for sire of cow and sire of insemination are estimated.

3.2. *Linear model*

After preliminary analyses concerning the significance of the effects of the percentage Holstein in sire of cow and sire of insemination, the effect of inseminator and the interaction of herd by year-season, the following model was used to estimate genetic parameters per parity.

$$\underline{y} = \underline{X}_1\underline{b}_1 + \underline{X}_2\underline{b}_2 + \underline{Z}_1\underline{u}_1 + \underline{Z}_2\underline{u}_2 + \underline{e}$$

where $\underline{y}$ = vector of observations on traits non-return (56 days), conception rate and days open (1*n)

$\underline{b}_1$ = vector with herd effects (fixed, $1*p_1$)

$\underline{b}_2$ = vector with year-season effects (fixed, $1*p_2$)

$\underline{u}_1$ = vector with effects of sire of cow (random, $1*q_1$)

$\underline{u}_2$ = vector of effects of sire of insemination (random, $1*q_2$)

$\underline{e}$ = error

$\underline{X}_1$, $\underline{X}_2$, $\underline{Z}_1$ and $\underline{Z}_2$ are incidence matrices, relating the effects

$\underline{b}_1$, $\underline{b}_2$, $\underline{u}_1$ and $\underline{u}_2$ to the observations, q_1 and q_2 are of the same length.

Four seasons per year were distinguished: Feb. - April (1), May-July (2), Aug.-Oct. (3) and Nov.-Jan. of the following year (4). July 1979, the first month for which data were available, was combined with season 3 of that year due to small numbers.

First and second moments of the random variables are as follows:

$$E\begin{bmatrix}\underline{y}\\ \underline{u}_1\\ \underline{u}_2\\ \underline{e}\end{bmatrix} = \begin{bmatrix}\underline{X}_1\underline{b}_1 + \underline{X}_2\underline{b}_2\\ \underline{0}\\ \underline{0}\\ \underline{0}\end{bmatrix}$$

$$V\begin{bmatrix}\underline{u}_1\\ \underline{u}_2\\ \underline{e}\end{bmatrix} = \begin{bmatrix}\underline{I}\,\sigma^2{}_1 & \underline{I}\,\sigma_{12} & \underline{0}\\ & \underline{I}\,\sigma^2{}_2 & \underline{0}\\ \text{symm.} & & \underline{I}\,\sigma^2{}_0\end{bmatrix}$$

and $V(\underline{y}) = \underline{Z}_1\underline{Z}_1{}'\,\sigma^2{}_1 + \underline{Z}_2\underline{Z}_2{}'\,\sigma^2{}_2 + (\underline{Z}_1\underline{Z}_2{}' + \underline{Z}_2\underline{Z}_1{}')\,\sigma_{12} + \underline{I}\,\sigma^2{}_0$

An extensive description of the model is given by Van Vleck and Johnson (1980).

Instead of an analysis by parity, the possibility of a multiple trait study with each parity as a separate trait was also considered. In case all cows in the data set would have a parity 0 record, this would also circumvent the possible effect of selection on the parameters. The limited number of cows having a heifer record as well as a second or third parity record prevented this analysis. Besides selection probably has only a minor effect, firstly because selection pressure is low, secondly mass selection on fertility is very inaccurate due to a low heritability and low repeatability of fertility measures. Therefore the first procedure was chosen.

3.3. Estimation of variance components

Let $\underline{G} = V\begin{bmatrix}\underline{u}_1\\ \underline{u}_2\end{bmatrix}$ then $\underline{G}^{-1} = \begin{bmatrix}\underline{I}\,\alpha_{11} & \underline{I}\,\alpha_{12}\\ & \underline{I}\,\alpha_{22}\end{bmatrix}$

Let $\underline{S} = \underline{I} - [\,\underline{X}_1\ \underline{X}_1\,]\begin{bmatrix}\underline{X}_1{}'\,\underline{X}_1 & \underline{X}_1{}'\,\underline{X}_2\\ \underline{X}_2{}'\,\underline{X}_1 & \underline{X}_2{}'\,\underline{X}_2\end{bmatrix}^{-1}[\,\underline{X}_1\ \ \underline{X}_2]'$

After absorption of herd and year-season effects the normal equations can be written as

$$\begin{bmatrix} \underline{Z}_1' \underline{S}\underline{Z}_1 + \underline{I}\,\alpha_{11}\,\sigma^2_0 & \underline{Z}_1' \underline{S}\underline{Z}_2 + \underline{I}\,\alpha_{12}\,\sigma^2_0 \\ \underline{Z}_2' \underline{S}\underline{Z}_1 + \underline{I}\,\alpha_{12}\,\sigma^2_0 & \underline{Z}_2' \underline{S}\underline{Z}_2 + \underline{I}\,\alpha_{22}\,\sigma^2_0 \end{bmatrix} \begin{bmatrix} \underline{u}_1 \\ \underline{u}_2 \end{bmatrix} = \begin{bmatrix} \underline{Z}_1' \underline{S}\underline{y} \\ \underline{Z}_2' \underline{S}\underline{y} \end{bmatrix}$$

Both $\underline{Z}_1$ and $\underline{Z}_2$ may contain columns with only zero's, since some sires may not have daughters and some sires may not have inseminations.
Let the inverse of the coefficient matrix be

$$\begin{bmatrix} \underline{C}_{11} & \underline{C}_{12} \\ \underline{C}_{12} & \underline{C}_{22} \end{bmatrix}$$

The order of this matrix is $q_1 + q_2$ ($q_1 = q_2$). REML-estimates of variance components can now be calculated as

$$\sigma^2_0 = (\underline{y}'\underline{y} - \underline{b}'\underline{X}'\underline{y} - \underline{u}'\underline{Z}'\underline{y}) \,/\, (N - r(\underline{X}))$$

$$\sigma^2_1 = (\underline{u}_1'\underline{u}_1 + \mathrm{tr}\ \underline{C}_{11}\,\sigma^2_0) \,/\, q_1$$

$$\sigma^2_2 = (\underline{u}_1'\underline{u}_2 + \mathrm{tr}\ \underline{C}_{22}\,\sigma^2_0) \,/\, q_1$$

$$\sigma_{12} = (\underline{u}_1'\underline{u}_2 + \mathrm{tr}\ \underline{C}_{12}\,\sigma^2_0) \,/\, q_1$$

Ordinary least squares estimates of σ^2_0, σ^2_1, and σ^2_2 were used as starting values, while σ_{12} was assumed to be 0 in the first round.

The EM-algorithm (Henderson, 1973) was modified to speed up the process of iteration. Instead of using the estimate of the last round as prior for the next round, the difference between the estimate of last and previous round times 2 was added to the new estimate of the genetic components. In theory this may lead to overshooting. Therefore the average of the estimates of the last and the previous round was used as prior for the next round when the sign of the difference between rounds changed.

$$\underline{G}^{*\,n}{}_{ij} = \underline{G}^{n}{}_{ij} + 2\,[\,\underline{G}^{n}{}_{ij} - \underline{G}^{n-1}{}_{ij}\,]$$

The following convergence criterion was used.

Calculate $\underline{G}^{n} - \underline{G}^{n-1} = \underline{A}$

Then let $x = \| \underline{A} \| = (\Sigma_i \Sigma_j a^2_{ij})^{.5}$ and $g = \| \underline{G} \|$ (Schaeffer, 1985).

Convergence was assumed when $(1-x/g) * 100$ was greater than 99.5.

3.4. Measurements of fertility

The fertility traits studied in parity 0 to 3 were: non-return rate at 56 days after first insemination, conception rate after first service and days open. 56 days non-returns were used instead of number of inseminations per service period, because these traits were genetically highly correlated (Janson, 1980) and non-return is currently used as a measure for fertility for sire of insemination in practice. Days open was included to study the combined effect of the interval between calving and first service and conception rate. Days open was replaced by age at conception in heifers. The estimates for the direct sire components of days open and age at conception may be affected by the fact that a cow may be reinseminated with another sire after failure to conceive at first service.

4. Results

Means and standard deviations of traits are given in table IV. Cows in first lactation were inseminated about three days later than second and third parity cows. Non-return and conception rates were higher than usually reported because animals with no subsequent calving date were not taken into account.

Table IV. Mean and standard deviation of traits by parity. (standard deviation is given in brackets. Those for non return and conception rate can be calculated as p * (1-p))

parity	interval calving-first insemination	non return 56 days	conception rate	days open
0[1]	462.4 (40.4)	76.8	73.1	476.2 (52.9)
1	80.2 (20.9)	74.5	69.4	96.6 (42.3)
2	77.4 (20.4)	72.2	67.6	93.6 (38.8)
3	77.1 (19.5)	71.5	67.0	93.7 (38.5)

1) parity 0: age at first insemination in stead of interval calving to first insemination and age at conception instead of days open.

Non-return and conception rates in heifers were clearly higher than those of primipari and multipari cows. Primipari also had higher non-return and conception rates than multipari, but this may partly be caused by a longer interval to first insemination (Berger et al., 1981). Estimates of (co)variance components for sire of cow and sire of insemination by trait by parity are given in table V.

Table V. Estimate of (co)variance components by trait and parity. Genetic components for non return and conception rate are multiplied by 10^4

trait	parity	sire of cow	covariance	sire of insemination	error	convergence
non return	0	0.40	0.56	9.20	0.175	99.52
	1	9.98	0.03	4.20	0.187	99.66
	2	11.78	4.26	7.53	0.197	99.52
	3	12.21	5.30	6.72	0.199	99.51
conception rate	0	0.87	-2.37	11.72	0.193	99.52
	1	5.01	0.04	8.67	0.207	99.50
	2	15.15	1.24	7.35	0.214	99.53
	3	13.51	5.07	8.01	0.215	99.51
age at conception	0	106.36	-1.18	22.89	2230.44	99.60
days open	1	6.50	0.14	0.49	1695.69	98.80[1]
	2	11.80	-1.11	2.73	1431.83	99.52
	3	18.01	0.81	1.00	1396.36	99.91

1) no convergence, OLS-estimate of sire of insemination < 0.

The sire of cow component for non-return and conception rate in heifers was smaller than the component of the sire of insemination (the LS-estimate was less than 0). The sire of cow component increased up to parity 2. The sire of insemination component showed no trend. The component for age at conception in heifers was expected as age at first insemination and age at conception depend on the size and development of the heifer. Both are known to be rather heritable. The covariance components increased with age, the covariance component for non-return rate in heifers being an exception.

The component for sire of insemination on days open was very small. After 15 rounds of iteration the convergence criterion had not been met in parity 1. Using OLS-procedures, neither one was significant when both were fitted, but both were significant when only one effect was fitted. This was probably due to the partial confounding of sire of insemination and year-season effects.

Table VI. Genetic correlations between sire of cow and sire of insemination components.

trait	parity			
	0	1	2	3
non return rate	-0.290	0.005	0.453	0.585
conception rate	-0.741	0.006	0.116	0.487
days open[1]	0.24	0.079	-0.196	0.191

[1] parity 0: age at conception

Genetic correlations between sire of cow and sire of insemination are given in table VI. For the traits non-return and conception rate these correlations changed from negative for parity 1 to moderately positive values for parity 3. For days open the trend was less clear.

Based on the estimates for the (co)variance components for sire of cow and sire of insemination heritabilities and genetic correlations of direct and maternal genetic components were calculated. Both direct genetic and maternal genetic components were small and showed no trend with parity (table VII). The genetic correlations, however changed from highly negative values in heifers to moderately positive values in parity 3 for non-return rate as well as conception rate. Days open did not show this trend.

Table VII. Heritabilities and genetic correlations of direct and maternal genetic components by parity

trait	parity	heritabilities		genetic correlations
		maternal	direct	
non return rate	0	0.007	0.021	-0.941
	1	0.023	0.009	-0.305
	2	0.019	0.015	0.059
	3	0.017	0.013	0.255
conception rate	0	0.013	0.024	-0.968
	1	0.013	0.013	-0.546
	2	0.029	0.013	-0.226
	3	0.019	0.015	0.117
age at conception	0	0.192	0.039	-0.248
days open	1	0.015	0.001	-0.059
	2	0.037	0.008	-0.406
	3	0.049	0.003	0.075

5. Discussion

Although the process of convergence was speeded up considerably, the criterion for convergence was hardly met within 10 rounds of iteration. Age at conception, a trait with a higher heritability, was an exception (3 rounds). The slow rate of convergence may partly be caused by the non-linear nature of the traits. A starting value of zero for the covariance component always implies a negative genetic correlation between the maternal and direct genetic components. Generally estimates of variance and covariance components may be dependent on the number of iteration rounds. In this study genetic correlation in heifers and primi pari hardly changed when iteration proceeded. The correlation for conception rate in parity 3, however, changed from -0.37 to +0.12 from round 1 to 11. Nevertheless the relative changes in the correlation between rounds were comparable to the changes in the components. The presented estimates will be close to the true REML-estimates, because a high degree of convergence was required.

The genetic correlations of non-return and conception rates between sire of insemination and sire of cow changed with parity. The changes were primarily due to the sire of cow component as a great deal of the inseminations in different parities comes from the same sires. These results confirm the findings of Hansen et al. (1983), who found low genetic correlations for number of services per period for sire of cow in heifers and first parity cows (.20 and .42). Janson (1980) and Distl (1982), however, found correlations close to 1. Genetic correlations between sire of cow and sire of insemination for parity 2 and 3 were close to values found by Hansen (1979) and Syrstad (1982). Although it would be tempting to improve fertility in cows via indirect selection on non-return rate of sires, the results indicate that this would not be effective for the improvement of conception rate in heifers and first parity cows. Indirect selection on non-return rates of sires would have a moderately positive effect on conception rates of older cows.

The background for the strong interaction between maternal and direct genetic effects in heifers and the changes with age was not clear. The direct component of variance contains the effect of the embryo on its survival as well as the effects of sperm quality. The maternal component comprises the effect of the uterine environment and egg quality. The impact of the different variables on fertilization and embryonic loss are not known yet. Changes in fertilization rate with age may have played a role. In heifers fertilization rate is almost 100%, at later ages this is reduced by 0-15% (Ayalon, 1981). This change may be related to the increase in metabolic rate when the cows start to produce milk. Another factor could be selection. However, direct selection for fertility in cows is not effective as previously discussed.

As the sire of insemination component contains also differences in semen quality, this component may be affected by differences in semen processing. Differences in semen processing usually tend to reduce differences in non-return rates between sires, because semen of bulls with high non-return rates is diluted more than that of bulls with poor results. The ranking of bulls is not necessarily affected. However, due to a reduced sire of insemination component, the direct genetic component will be underestimated and estimates of the maternal component and the covariance between direct and maternal effect may be affected as well. This problem cannot be solved with field data. It exists however, in all parities and therefore the interesting feature of changes in the covariance component with age remains.

For non-return and conception rate the heritabilities of the two components were about equal, for days open the direct component was smaller than the maternal component. In addition to genetic differences in uterine environment and egg quality the maternal component for days open also contains genetic variation in the interval between calving and first service. Therefore the direct component may be smaller. Reinsemination with semen of another sire may have played a role.

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Chapter 4

GENETIC RELATIONSHIPS BETWEEN FERTILITY TRAITS IN FRIESIAN COWS IN DIFFERENT PARITIES

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Abstract

Genetic relationships between fertility measurements in heifers and cows in parity 1, 2 and 3 were studied using a multivariate linear model with unequal design. Genetic parameters were obtained via a REML-procedure, accounting for selection. Components of variance increased by parity, especially for 56 days non-return rate. Genetic correlation between age at first insemination in heifers and interval to first service in first parity cows was 0.67, that for age at conception and days open 0.66. Genetic correlations between interval to first service in parities 1, 2 and 3 varied from 0.78 to 0.89, whereas relationships between days open varied from 0.68 to 1.06. Genetic correlations between non-return rates were all above unity. Culling hardly affected the parameter estimates for fertility.

1. Introduction

Evaluation of sires for daughter fertility is practised in some European countries. In Sweden the number of inseminations per service period is used as criterion for fertility and data of both heifers and first parity cows are considered, in Norway and Denmark non-return rates are evaluated, based on data of cows only (Janson, 1980b).

It would be preferable when data of both heifers and first parity cows could be used for sire evaluation. In that case a rather accurate sire evaluation might be obtained at the same time when the evaluation results for milk production in first lactation are available. Selection on female fertility based on measurements taken at an early age, however, is only meaningful when the relationship with fertility at an older age is high. Fertility problems seem to become greater at older ages. Culling due to fertility problems increased with age (Dijkhuizen, 1980) and insemination results decreased (Jansen and Lagerweij, 1986).

Reports on the association of fertility in heifers and first parity cows have been conflicting. Janson (1980a) found that 56 days non-return rate as well as number of inseminations per service period in Swedish cattle were highly correlated (r_g = 0.6-1.0). Distl (1982) reported similar values in Simmental cattle. Hansen et al. (1983c), however, obtained much lower values (0.1 to 0.3 in Holsteins). In these studies estimates were based on Henderson's method III.

Additionally relationships of fertility in first parity and later parity cows are not known. Jansen (1986) found that the genetic association between the sire of cow and sire of insemination component for 56 days non-return rate changed with age of the cow and suggested that the genetic correlation between fertility measured in heifers and first parity as well as in first parity and later parities differed from unity.

Estimates of variances and covariances may be biased due to selection (Cochran, 1951). Culling for fertility problems is the main reason for disposal in dairy cattle in Western Europe (Dijkhuizen, 1980; Philipsson, 1981). It is not possible to account for selection with the methods used hitherto, but a maximum likelihood (ML) or a restricted maximum likelihood procedure (REML) will do, if the information determining the selection decision is included in the analysis (Curnow, 1961; Meyer and Thompson, 1984).

In this study relationships between fertility traits in different parities were quantified. Attention was paid to the effect of selection on the estimates of genetic parameters.

2. Material and methods

The Friesian Cattle Syndicate (FRS) provided breeding receipts of 326 herds, spanning July 1, 1979 to February 29, 1984. Insemination data were matched with registration and milk recording data. Details of data audit are given in Jansen (1986). Records of heifers and cows in parity 1, 2 and 3, respectively were used for further analysis. Records with natural service were removed.

The following measurements of fertility were considered

- age at first insemination and age at conception in heifers
- 56 days non-return rate after first insemination in both heifers and cows (parity 1, 2 and 3)
- calving to first service interval and days open in cows.

To determine age at conception and days open the subsequent calving date had to be known. Selection can be practised within and between parities. Selection within parity for example takes place when a first insemination is known after calving, but no subsequent calving date. Selection between when a second calving date is known, but no subsequent first insemination date.

Due to selection within parities, the number of records analysed for age at conception in heifers and days open in cows will always be less than the number for the other traits in a particular parity.

The REML procedure which was used to estimate (co)variance components (see next section), will account for the possible effect of selection on the genetic parameters, if the information determining the selection decision is included in the model. This means that all animals should have a heifer record. In our study we considered only selection from parity 1 onwards. There were not enough heifer records available to consider selection from parity 0 onwards. Partly because many records were lost due to lack of sire identification, partly due to the use of natural service in heifers.

Selection on fertility in heifers is expected to play a minor role due to high conception rates obtained after first service. Besides fertility traits in heifers may be different, partly because interval traits in heifers are defined in a different way and also because milk production does not play a role yet.

Genetic parameters were analysed for two traits at the time. A trait was defined as a combination of measurement and parity. Only corresponding measurements in different parities were considered in order to reduce the costs of computation, i.e. 56 days non-return rate in heifers and cows, calving to first service interval in cows, days open in cows, age at first service in heifers in relation to interval to first service in parity 1 and age at conception in heifers in relation to days open in parity 1.

For every analysis seperate data selections were carried out to contain as much information as possible. When relationships between parities 1 and 2, 1 and 3 and 2 and 3 were analysed, records of the latter parity were only used if a record of the previous parity was available.

Sires were required to have at least 9 progeny records in different herd-year-seasons. The maximum numbers of sires which could be handled by the algorithm used, was 178 sires. When the number of sires remaining was greater than 178, the smallest progeny groups were removed ad random. When the total number of records per herd was greater than 151 (the maximum set in the computer program) records were removed ad random until this number was reached. Table I summarises the results of the different selection steps.

Table I. Number of records used in the analyses.

	parity			
	0	1	2	3
records with known sire	10285	14951	11996	9039
pairwise analysis A				
parity 0-1	8856	4472	-	-
parity 1-2	-	12051	6307	-
parity 1-3	-	12145	-	2796
parity 2-3	-	-	9640	4985
pairwise analysis B				
parity 0-1	7858	3905	-	-
parity 1-2		10517	5436	-
parity 1-3		10580	-	2307
parity 2-3		-	8276	4145

A : traits age at first insemination in heifers, interval calving to first insemination and 56 days non-return

B : traits age at conception in heifers and days open.

2.1. *Multivariate linear model*

A multivariate linear model with unequal design was used for the analysis. This allows the design for the two traits on the same animal to differ and information on a trait to be missing. It will account for selection if the information used for the selection decision is included. The model was as follows:

$$y = X\beta + Zu + e$$

where y = vector of observations on corresponding traits in two parities
β = vector of fixed effects
u = vector of random sire effects
e = vector of residuals

The vector y contains the information on both traits. X and Z are the design matrices for the fixed and random effects.

Three fixed effects were used: herd, group of descendance (purebred Dutch Friesian or Holstein (including crossbreds)) and year-season. Four seasons per year were considered: Feb. - April (1), May - July (2), Aug. - Oct. (3) and Nov. - Jan. of the following year (4). July 1979, the first month with data, was combined with season 3 of that year due to small numbers.

First and second moments are

$$E\begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}$$

and

$$V\begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} ZGZ'+R & GZ' & R \\ & G & 0 \\ \text{symm.} & & R \end{bmatrix}$$

The mixed model equations to estimate fixed and random effects were (Henderson, 1973)

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z \end{bmatrix} \begin{bmatrix} \beta \\ u \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

2.2. *Estimation of variance and covariance components*

A restricted maximum likelihood procedure (REML) was used to estimate the variance and covariance components from the multivariate mixed model with unequal designs for the traits. The details are described in Meyer (1986). The algorithm uses the expectation maximisation method to estimate the within random effects components and the method of scoring to estimate the between components. To speed up the process of iteration a so called k-transformation was used (Meyer, personal communication, 1986).

Estimates according to Henderson's method III were used as starting values. Iteration was stopped after five rounds. By then the change between rounds was smaller than 1%, except for non-return rate. Estimates of genetic correlations, however, hardly changed in the last round of iteration.

2.3. *Effects of selection and unequal design*

The advantages of the use of a multivariate linear model with unequal design have been described before. The effects of the three components were quantified for estimates of parity 1-2. Four alternatives were considered.

A. use of all information, unequal design for fixed effects (the base model, also used for all other analyses)

B. as A, but removal of cows which had no opportunity for a parity 2 record

C. as B, but removal of parity 1 cows, which had been culled. So only cows with two traits were taken

D. as C, but equal design for both traits. The design was based on trait 1.

The numbers for the different alternatives are given in table II.

Table II. Number of records used in the comparison of methods (for A,B,C, and D see text).

method	interval to first service 56 days non-return rate		days open	
	parity 1	parity 2	parity 1	parity 2
A	12051	6307	10571	5436
B	7841	6307	6307	5436
C and D	6307	6307	5436	5436

3. Results and discussion

Because different subsamples were used from the data set, different parameter estimates were obtained for some traits. Estimates from the largest data set will be presented, except for estimates of genetic (co)variances, which will all be presented.

Overall means and standard deviations of traits are given in table III. The means are consistent with other samples taken from the same data set (Jansen, 1986). Differences between means of the different subsamples were neglectable.

Table III. Overall means and standard deviations of traits by parity. (standard deviations in brackets. Those for non-return rate can be calculated as p*(1-p)).

parity	interval calving to first service	56 days non-return rate	days open
0[1]	463.3 (40.5)	76.1	476.1 (52.6)
1	80.8 (20.6)	71.6	97.9 (42.0)
2	77.0 (20.0)	70.6	93.3 (38.5)
3	76.0 (20.1)	69.1	91.7 (38.7)

[1] parity 0 : age at first insemination instead of interval to first service and age at conception instead of days open.

Table IV. Phenotypic correlations between corresponding fertility traits.

	interval to first service[1]	56 days non-return rate	days open[1]
parity 0-1	0.020	0.049	0.014
parity 1-2	0.098	0.060	0.061
parity 1-3	0.092	0.055	0.226
parity 2-3	0.086	0.071	0.070

[1] parity 0 : age at first insemination instead of interval to first service and age at conception instead of days open.

Table IV contains the phenotypic correlations between corresponding traits in different parities. Correlations between traits in parity 1, 2 and 3 can be considered as repeatabilities. Except for days open in parity 2-3, correlations were less than 10%. Estimates were in the lower range of values found by Hansen et al. (1983a) and Maijala (1964). Because days open and calving interval are highly correlated, similar values are to be expected for calving interval.

Estimates of sire components of (co)variance are presented in table V. Repeated estimates for interval to first service were rather consistent, except for parity 3. Variances increased with parity number. The genetic variation for 56 days non-return rate in heifers was about zero. Repeated estimates were consistent for parity 1, but differed highly for parity 2 and 3. Similar results were obtained for days open. Sampling should be the main cause for the differences between repeated estimates. The lower bound standard errors corresponded very well to the numbers involved in the different estimates.

Table V. Sire components of (co)variance and lower bound standard errors (standard errors in brackets).

Interval to first service[1]			
	variance[a]	covariance	variance[b]
parity 0-1	79.81 (10.45)	9.99 (2.78)	2.77 (1.13)
parity 1-2	2.53 (0.69)	2.90 (0.74)	5.20 (1.30)
parity 1-3	2.56 (0.70)	3.95 (1.12)	9.92 (2.80)
parity 2-3	4.95 (1.07)	5.10 (1.08)	6.65 (1.68)
56 days non-return rate (multiplied by 10^4)			
	variance	covariance	variance
parity 0-1	0.30 (1.69)	4.66 (2.16)	5.43 (4.58)
parity 1-2	5.82 (2.16)	9.62 (2.27)	4.11 (2.88)
parity 1-3	6.01 (2.46)	3.49 (3.91)	8.01 (9.87)
parity 2-3	10.54 (3.29)	19.62 (4.38)	28.12 (7.93)
days open[1]			
	variance	covariance	variance
parity 0-1	96.35 (15.03)	20.63 (7.16)	10.27 (5.39)
parity 1-2	6.51 (2.49)	4.55 (2.17)	6.97 (3.36)
parity 1-3	6.87 (2.65)	13.45 (3.93)	23.24 (8.83)
parity 2-3	15.59 (4.06)	10.01 (1.60)	13.50 (5.43)

[1] parity 0 : age at first insemination instead of interval to first service and age at conception instead of days open.

[a] and [b] : former and latter parity respectively.

Estimates of heritabilities and genetic correlations are given in table VI. The heritability for interval to first service increased from 0.03 in parity 1 to 0.12 in parity 3. Estimates for parity 2 and 3 as well as the genetic correlation between age at first service and interval to first service in first parity cows were higher than those reported by Hansen et al. (1983b). This may reflect differences in management conditions. Genetic correlations between interval to first service in cows varied between 0.78 to 0.89.

Table VI. Heritabilities and genetic correlations

	heritability	genetic correlation with parity 1	2	3
Interval to first service[1]				
parity 0	0.246	0.672	-	-
parity 1	0.032		0.798	0.784
parity 2	0.061			0.889
parity 3	0.115			
56 days non-return rate				
parity 0	0.001	3.662	-	-
parity 1	0.011		1.968	0.502
parity 2	0.008			1.139
parity 3	0.016			
days open[1]				
parity 0	0.167	0.656	-	-
parity 1	0.025		0.676	1.065
parity 2	0.021			0.690
parity 3	0.070			

[1] parity 0 : age at first insemination instead of interval to first service and age at conception instead of days open.

The estimates of genetic correlations between parities for 56 days non-return rate were out of bounds. As discussed by Meijering (1985), this is probable due to the fact that a binary trait is analysed with a linear model. He concluded that this results in sire components of variance which are underestimated and therefore the genetic correlation can easily be estimated out of bounds. On the other hand, the algorithm used may play a role as well. Henderson's method III gave estimates closer to 1 in an analysis of a subset. Generally estimates of genetic correlations are expected to be unbiased as shown both theoretically and emperically (Mao, 1976; Gianola, 1982).

The estimate for age at conception in heifers was somewhat lower than for age at first service (0.25 versus 0.17). In contrast to Hansen et al. (1983c) the correlation between age at conception and days open in first parity cows was highly positive (0.67 versus -0.16 as reported by Hansen et al.). Genetic correlations between days open in parities 1, 2 and 3 were 0.7, except for parities 1-3. Days open is determined by both interval to first service and conception results. Because the correlations between interval to first service was somewhat higher than for days open, it could be speculated that the true genetic correlation for non-return rates in different parities is somewhat lower than unity. The sire components of variance increased also by parity, indicating that different genes may be expressed.

Table VII. Means of traits in parity 1 in different subsets.
(for A, B, C and D see text)

subset for method	interval calving to first service	56 days non-return rate	days open
A	80.4	72.9	96.5
B	80.3	73.3	93.5
C and D	80.2	75.5	93.6

The means of the data used for the comparison of the different methods are given in table VII. The base set (A) containing also information of animals, which did not have the opportunity for a second parity record, had lower 56 days non-return rates and longer days open than the data set in which these animals were removed (set B). The comparison of data set B versus C and D shows that animals which were culled during or after first lactation, had considerably lower non-return rates (64.1 versus 75.5%), but did not differ in interval to first service.

Table VIII. Sire components of (co)variance from different subsets for parity 1 and 2 (for A, B, C and D see text).

Interval to first service			
	variance[a]	covariance	variance[b]
A	2.54	2.90	5.20
B	3.11	3.76	5.59
C	3.05	3.78	6.38
D	2.48	1.83	2.84
56 days non-return rate (multiplied by 10^4)			
	variance	covariance	variance
A	5.82	9.62	4.11
B	5.45	10.97	7.99
C	6.84	14.23	11.58
D	9.04	14.35	9.60
days open			
	variance	covariance	variance
A	6.51	4.55	6.97
B	16.61	5.66	6.62
C	20.49	6.76	7.07
D	20.27	7.05	8.58

[a] and [b] : former and latter parity respectively

The genetic variances and covariances for the different sets are given in table VIII. Removal of data of animals which had no opportunity for a second parity had clear effects on the variance of days open. The comparison of B, C and D gave ambiguous results. One would expect that variance and covariance components would decrease when no information on culled cows would be used (B versus C) and when the design for the second trait would be less optimal (C versus D). This trend was observed for interval calving to first service, but not for 56 days non-return rate and days open. The genetic correlation decreased somewhat for interval to first service (0.902, 0.858 and 0.689 for B, C and D, respectively) and non-return rate (1.66, 160 and 1.54) but not for days open (0.54, 0.562 and 0.531). From comparing B and C it was concluded that the effect of culling on fertility on the genetic parameters was neglectable. Partly this may be caused by the low heritability of the traits. The effect of a less optimal design (D versus C) depends also on the confounding of fixed effects and the sire effects.

Our results do not confirm the low relationships between heifer and first parity fertility found by Hansen et al. (1983c), but are consistent with Janson (1980a) and Distl (1982). In addition relationships with fertility in parity 2 and 3 were high, although not equal to 1. Therefore results of heifers and first parity cows can be used for the evaluation of fertility of progeny groups.

Besides 56 days non-return rate, the number of inseminations per service period was used by Janson (1980a) and Haug (1985). This measure as well as the measurements interval to first service and days open showed higher heritabilities than non-return rate. Besides biological effects "preferential" treatment may be involved. Van Arendonk and Dijkhuizen (1985) showed that it could be profitable to continue inseminating for a longer period with high procedures and also to postpone first insemination in high producing cows from parity 3 onwards. This will always inflate heritability estimates. These effects, however, cannot be accounted for in the analysis of field data, but should be considered in the choice of traits. Non-return rate is less affected although some low producers may not be inseminated at all. This trait is to be preferred therefore as measure of fertility to be evaluated.

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Chapter 5

PARAMETERS TO MONITOR DAIRY HERD FERTILITY AND THEIR RELATION TO FINANCIAL LOSS FROM REPRODUCTIVE FAILURE

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Abstract

Relationships between herd fertility measurements and financial loss from reproductive failure in dairy herds were studied. Financial losses attributable to prolonged calving interval and forced replacement from reproductive failure were considered. Herd fertility parameters were calculated from artificial insemination and calving data, i.e. calving to first service interval, non-return rate 56 days after first service, percentage correct inseminations done in the interval 18-24 days, fertility status, calving interval, an oestrus index and number of inseminations per average cow present in the herd.

The herd fertility parameters were moderately to highly related to loss due to suboptimal calving interval (r= 0.20 to 0.79 in absolute values), but only slightly related to losses due to forced replacement (r was less than 0.17 in absolute values).

Repeatabilities calculated over a three year period, were high for the interval to first service, non-return rate and the oestrus index (0.52 to 0.67), moderate for percentage correct reinseminations, fertility status, calving interval and loss due to suboptimal calving interval (0.38 to 0.48). Repeatability of loss due to forced replacement was low (0.20).

In a regression analysis no herd fertility parameter was fitted with respect to loss from forced replacement. Loss due to suboptimal calving interval at herd level was best estimated by the oestrus index (R^2= 0.63), the addition of the interval to first service to the regression equation explained a further 10% of the variation between herds. It is suggested to present the oestrus index and the interval to first service as management aids to monitor herd fertility.

1. Introduction

Reproductive failure causes considerable financial losses in dairy herds. Model calculations by Dijkhuizen et al. (1985a) showed an average loss of Dfl. 63 per cow per year. The calculated loss included loss due to prolonged calving interval (Dfl. 35.50) and loss due to forced replacement (Dfl. 27.50). There were large differences between farms, mainly due to differences in forced replacement.

Different parameters have been used to monitor herd fertility. In herd health programs use has been made of the "fertility status" (De Kruif, 1975). This parameter requires a pregnancy check. Dairy Herd Improvement Organizations may present an average calving interval. Parameters derived from AI (artificial insemination) data have also been used (Warren, 1983). Drees (1982) reported repeatabilities of yearly averages of 0.23 and 0.11 for the interval calving to first service and conception rate, respectively. Repeatabilities of a two year rolling average for these measures were 0.52 and 0.38, respectively. Use of AI data would provide the opportunity to calculate herd fertility figures routinely and on a wide scale.

An important imperfection of previously discussed parameters is the fact that forced replacement due to reproductive failure is not taken into account, except for the modified fertility status by Esslemont and Eddy (1977). They may even be biased upwards by early disposal of problem cows. Furthermore it is unknown to what extent these parameters contribute to the financial loss due to reproductive failure.

In this study relationships of herd fertility parameters calculated from AI data, with the financial loss due to reproductive failure at the farm level will be quantified. Attention will be paid to the factors which can be used to monitor herd fertility routinely and on a wide scale, and are related to the herdmanship of the dairy farmer. Repeatability of herd fertility will be included to determine whether herd management can be characterised consistently.

2. Materials and methods

Data were collected on 33 herds participating in a herd health and management program, and 32 herds used as control farms. An extensive description of the selection procedure of program and control farms and the herd health and management program itself is given by Sol and Renkema (1984). Records with a calving interval less than 300 or greater than 525 days were removed. In total 13644 records with calving dates and subsequent AI data were available for analysis, covering the period May 1974 to April 1977. The following herd fertility parameters were calculated:

- interval calving to first service (interval to first service)
- non-return rate 56 days after first service (non-return rate)
- percentage of the reinseminations done in the interval 18-24 days (percentage correct reinseminations)
- fertility status, calculated as (percentage diagnosed pregnant after first service divided by the number of inseminations per conception) - (days open-125) (De Kruif, 1975)
- calving interval
- oestrus index. The oestrus index determined the number of oestri per inseminated cow, wrongly interpreted or missed by the farmer. The numbers were summed over cows and divided by the number of inseminated cows. The number per cow was derived from the following intervals, modified after Elving and Van Eldik (1985):

  - interval to first service. First the herd average was calculated. The number of oestri per cow that was missed or wrongly interpreted equaled (interval to first service - herd average to first service +10) divided by 21, truncated (only positive numbers were used).
  - interservice interval 4-17 days: 1 oestrus wrongly interpreted
  - interservice interval 26-36 days: 1 oestrus missed or wrongly interpreted.
  - interservice interval greater than 36 days: the number equaled (interval divided by 21)-1, rounded to the nearest integer

  (When the number of correct inseminations is also summed i.e. one insemination per cow, inseminations in the interval 18-24 days and one insemination in the interval 26-36 days, the oestrus (detection) rate can be calculated as number of correct inseminations divided by (number of correct inseminations plus number of missed and wrongly interpreted oestri).
- number of inseminations per average cow present in the herd per year (number of inseminations).

In addition to these variables also the percentage culled due to reproductive failure and low production were calculated.

The calculation of financial loss due to suboptimal calving interval and forced replacement caused by reproductive failure is described in detail by Dijkhuizen et al. (1985a, 1985b). The loss due to suboptimal calving interval was derived from the distribution of the length of the interval for the herd. The calculation of financial loss from forced replacement was based on expectations about milk yield, fat and protein percentage, feed costs, calf sales, probability of disposal and opportunity costs of postponed replacement. The latter equalled the expected revenues from a replacement heifer over the period of time the cow is expected to stay in the herd. The criteria to cull were made by the farmer.

Repeatabilities of herd fertility measures between years were calculated using correlation analysis. Repeatability over the total period of three years was calculated from a linear model including year and herd. Repeatability can then be calculated as

$$\sigma^2_n / (\sigma^2_n + \sigma^2_e)$$

where

σ^2_n = component of variance due to herds

σ^2_e = error component.

Regression analysis was done to determine the accuracy of prediction of loss. Variables such as days open, calving interval and fertility status have the disadvantage of being calculated after the interval to first service and success of insemination are known. Therefore these variables were not used in the regression analysis. Instead variables were used which are up to date and more directly related to the decisions made by the farmer to get his cows pregnant: interval to first service, non-return rate, percentage correct reinseminations and oestrus index. A default stepwise regression procedure was used as described by Nie (1975).

Because data were available from both program and control herds it was first studied whether the herd health program had an effect on the relationships between herd fertility parameters and financial loss. The relationships between herd fertility measurements and financial loss were not influenced and therefore the program and control herds were pooled. A possible effect of the program would have inflated the correlations, but would lower the accuracy of estimation, measured by the mean square error.

3. Results

3.1. Means and variation

Means, standards deviations, minima and maxima of the herd fertility parameters, averaged over a three year period, are given in Table I. About 47% of the reinseminations were done in the period 18-24 days after a previous service. An oestrus index of 0.80 indicates that per average cow present in the herd almost one oestrus is missed or wrongly judged. The contribution of the different intervals was as follows: interval to first service 0.38; interservice interval 4-17 days 0.05; interservice interval 26-36 days 0.05 and intervals greater than 36 days 0.32. The relation between oestri missed before first service and those missed with long interservice intervals was 0.64.

There were large differences between herd means, e.g. non-return rate varied from 52.8% to 83.2%, the oestrus index varied from 0.37 to 1.73.

3.2. Relationships between herd fertility variables

Correlations between herd fertility variables are presented in Table II. Interval to first service, fertility status and the oestrus index were strongly correlated with the calving interval at herd level (r= 0.67, -0.64 and 0.60, respectively). Non-return rate showed no significant relation, whereas the correlation of percent correct reinseminations with calving interval was -0.36. The percent correct reinseminations and the oestrus index were highly correlated (-0.59).

Table I. Mean, standard deviations, minima and maxima of herd fertility variables and financial loss (n=65)

	mean	s.d.	min.	max.
no of cows	65.0	25.4	29.1	172.3
interval to first service (days)	78.2	6.2	66.	91.2
non-return rate (%)	67.8	7.2	52.8	83.2
percent correct reinseminations (%)	47.4	8.6	26.2	67.4
fertility status	77.7	14.2	30.2	103.2
calving interval (days)	372.2	8.6	348.7	406.5
oestrus index	0.80	0.24	0.37	1.73
inseminations per cow	1.58	0.19	1.17	1.95
culled for reprod. failure (%)	25.3	9.1	2.3	41.8
culled for low production (%)	21.9	11.3	5.3	55.3
losses due to reprod.failure (Dfl.)				
suboptimal calving interval	34.50	10.00	16.00	65.50
forced replacement	30.00	19.00	0.50	86.50
total loss	64.50	20.50	23.50	128.00

Table II. Correlations between herd fertility variables.

	variable							
	1	2	3	4	5	6	7	8
1. interval to first service								
2. non-return rate	0.37							
3. perc. correct reinseminations	-0.24	-0.29						
4. fertility status	-0.08	0.65	0.02					
5. calving interval	0.67	-0.02	-0.36	-0.64				
6. oestrus index	0.25	-0.17	-0.59	-0.53	0.60			
7. inseminations per cow	-0.37	-0.78	0.16	-0.56	0.04	0.32		
8. culled for fertility	0.01	-0.26	-0.27	-0.13	-0.14	0.24	-0.10	
9. culled for low production	-0.01	0.20	0.07	0.09	0.02	-0.13	-0.22	-0.42

($r > 0.24$: $p < 0.05$; $r > 0.31$: $p < 0.01$)

Parameters calculated from AI data were only slightly related to percentage culled for reproductive failure. Significant correlations were found for non-return rate, percent correct reinseminations and the oestrus index (-0.26, -0.27 and 0.24, respectively). No significant correlations were found between herd fertility variables and the percent culled for low production. However, the percent culled for low production and culled for fertility problems was significantly correlated (-0.42).

This may be due to a difference in use of criteria to cull cows. Therefore a canonical correlation analysis was performed, in which the frequencies of disposal due to reproductive failure and low production were related to herd fertility parameters. Although the first factor was not significant ($p = 0.14$), the weights for frequency of disposal for reproductive failure and low production were about equal, but differed in sign.

3.3. *Repeatabilities*

Repeatabilities of herd fertility parameters are given in Table III. The interval to first service, non-return rate and oestrus index showed the highest repeatabilities. Values over a three year period were 0.58, 0.52 and 0.63, respectively. Repeatability of losses due to forced replacement was low (0.20). Values for the other variables were intermediate.

Table III. Repeatability of herd fertility variables

	year 1-2	year 1-3	year 2-3	total period
interval to first service	0.73	0.46	0.59	0.58
non-return rate	0.67	0.47	0.39	0.52
perc. correct reinseminations	0.41	0.43	0.49	0.43
oestrus index	0.59	0.56	0.73	0.63
fertility status	0.36	0.34	0.44	0.38
calving interval	0.46	0.32	0.59	0.45
losses due to				
suboptimal calving interval	0.50	0.31	0.62	0.48
forced replacement	0.45	0.14	0.11	0.20
total loss	0.45	0.15	0.28	0.25

3.4. *Relations herd fertility variables and financial loss*

Financial loss due to suboptimal calving interval and forced replacement were hardly related (-0.05). The correlation of these factors with total loss was 0.43 and 0.88 respectively. Correlations between financial loss due to reproductive failure and herd fertility parameters are given in Table IV.

Table IV. Correlations between herd fertility variables and financial losses due to reproductive failure

	financial losses		
	suboptimal calv.interval	forced replacement	total
interval to first service	0.52	0.16	0.39
non-return rate	-0.20	0.02	-0.07
perc. correct reinseminations	-0.36	-0.12	-0.28
fertility status	-0.67	0.17	-0.16
calving interval	0.77	-0.11	0.26
oestrus index	0.79	0.15	0.51
inseminations per cow	0.24	-0.08	0.04
culled for low reproductive failure	0.09	0.66	0.64
culled for low production	-0.11	-0.32	-0.34

($r > 0.24$: $p < 0.05$; $r > 0.31$: $p < 0.01$)

Relationships of losses due to suboptimal calving interval with fertility measures were significant, except for non-return rate and frequencies of culling for reproductive failure and low production. On the other hand loss due to forced replacement caused by reproductive failure showed hardly any relation with parameters derived from AI data, but was significantly influenced by culling due to reproductive failure as was to be expected (0.66). Culled for low production also had a significant, but negative correlation with loss due to forced replacement (-0.32).

3.5. *Regression analysis*

Regression analysis was done with data averaged over a three year period. Coefficients of determination are given in Table V. As could be expected from the correlation coefficients the accuracy of estimation of loss due to suboptimal calving interval was rather good. After the oestrus index was fitted, the interval to first service and non-return rate still improved the equation substantially. The maximum R^2 achieved when the remaining variables (calving interval etc.) were also fitted, was 0.83. As expected no variable was fitted with respect to loss due to forced replacement. The total loss was significantly influenced by the oestrus index and the interval to first service. As total loss was calculated as the sum of loss due to suboptimal calving interval and loss from forced replacement, the accuracy of prediction was rather low.

Table V. Coefficients of determination (R^2) of financial losses due to reproductive failure. Significant variables are listed in order of selection

A. losses due to suboptimal calving interval	
sequence of selection	R^2 (cumulative)
1. oestrus index	0.63
2. interval to first service	0.73
3. non-return rate	0.79 error mean square 20.82
B. losses due to forced replacement: no variables fitted	
C. total loss	
sequence of selection	R^2 (cumulative)
1. oestrus index	0.26
2. interval to first service	0.33 error mean square 294.30

4. Discussion

The differences in repeatabilities obtained indicate that some herd fertility parameters are more useful to characterise herdmanship than others. It is difficult to state what the lower limit should be and what upper limit is obtainable. This depends also on the length of the period considered, as was shown by Drees (1982). The repeatabilities found in this study were considerably higher than in Drees' study. For milk production repeatabilities of herd yearly averages of 0.85 to 0.90 have been found (Wilmink, personal communication, 1985). From figures given by Mao (1976) a repeatability of 0.67 for herd milk production could be calculated. In the present study figures for the interval to first service, non-return rate and oestrus index were close to the latter figure. When forced replacement was involved, repeatability was low. A low repeatability may also be caused by the small number of cows disposed of annually in small herds. However, the size of the changes between years could not related to farm size. Differences in herds with respect to losses due to forced replacement were not explained accurately by herd fertility measures. Although herds with poor fertility were expected to have more loss, factors related to decisions made by the farmer, were poorly related to this loss. In addition to differences in use of culling criteria as indicated by the canonical correlation analysis, there may also be differences in relative level at which cows are disposed of when they are culled for reproductive problems. These factors may have reduced the accuracy of estimation. Further research on factors contributing to differences in loss due to forced replacement is needed before this figure can be used in monitoring herd fertility. In addition to replacement rate and relative level of production, this should include the effect of season and differences in calving pattern on the farms. Seasonal variation in milk production influenced the optimum replacement policy in dairy herds (Van Arendonk, 1985).

The quality of oestrus detection is probably the most important factor determining differences in herd fertility. Poor heat detection increases the average calving interval, as well as the percentage culled due to reproductive failure (Esslmont, 1982). The approximate oestrus detection rate in this study was 60% (standard deviation of 6%). This is about 10% higher than reported in British data (Esslmont and Eddy, 1977). In addition to inseminating at the wrong time, losses are also due to cows not detected in heat but suitable for insemination. Zemjanis et al. (1969), cited by O'Farrell (1982) found that 90% of the cows being reported anoestrus, were in fact cycling and presumably were missed due to errors in heat detection. This category comprised about 10-12% of all cows (O'Farrell, 1982).
The oestrus index discussed before combines the number of missed oestri before first service and wrongly interpreted or missed oestri afterwards. The oestrus index may be inflated by late embryonic loss and post insemination anoestrus. However 80% of the cows not pregnant, return to cycling within 25 days (Humblot, 1982). Differences between herds in late embryonic death and post insemination anoestrus will therefore play a minor role.

The oestrus index showed a high relation with the loss due to suboptimal calving and had also a high repeatability. Therefore it is recommended to present this figure to the farmer. Additionally the average interval to first service may be presented, as this was also an important component explaining differences with respect to losses due to suboptimal calving interval between herds. This is supported by Williamson et al. (1980) and Dohoo(1983) who found that a 1-day reduction in interval to first service reduced the calving interval and days open with 0.86 days. Both the oestrus index and interval to first service can be calculated on the basis of calving and insemination data and are directly related to decisions made by the farmer. In herd health programs the value of the oestrus index may be further improved by the inclusion of actual oestrus data.

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GENERAL DISCUSSION

The research on the analysis and use of AI-data described in this thesis, can be distinguished in two main areas. The first focussed on the genetic aspects of fertility. These aspects have been dealt with in the literature review (chapter 1) and also in the studies on the relationships between male and female fertility (chapter 3) and fertility of cows in different parities (chapter 4). The second area was directed to the use of AI information for management purposes. On the one side this is in the interest of the AI-organization with respect to evaluation of insemination results of bulls and technicians (chapter 2). On the other side it is of interest for the dairy farmer with respect to the choice of bulls with positive non-return rates (chapter 2) and the evaluation of his own management (chapter 5).

In each of the papers the main results have already been discussed. This general discussion will be confined to the following issues:

- methodology used in the different chapters
- the relationship between male and female fertility
- conclusions with respect to the evaluation and use of AI information.

Methodology

The fertility traits analysed have either a discrete distribution (non-return rate, conception rate) or are continuous ones, but somewhat skewed (interval traits e.g. days open). Mixed linear methodology was used throughout the study, although the condition of normality for the error terms and random effects was not met. The consequences should be considered in two ways.

Firstly it has been shown (Gianola, 1982) that heritability of traits with a categorical nature and phenotypic correlations between categorical (and continuous) traits are underestimated. Formulas to transform these parameters to the underlying scale are given in Gianola (1982). When heritabilities of 56 days non-return and conception rate would be transformed to the underlying continuous scale, these would be increased by 60 to 75%. Nevertheless heritabilities would be less than 4%, which is still low. The effect on the variances of the estimates are not known, but it is not unlikely that these are overestimated. Repeatabilities of these traits were also underestimated (about 30%), but were never above 20% when transformed to the underlying continuous scale. With respect to estimates for traits with a skewed distribution, Banks et al. (1985) showed that a REML algorithm yielded unbiased estimates, but variance estimates increased. In our study the skewness of the interval traits was reduced because lower and upper bounds were set on these traits.

The second point of greater concern, is whether the methodology used in this study results in a lower efficiency of sire selection. Meijering and Gianola (1985) showed that the difference in efficiency of selection between a mixed linear model and a non-linear model was dependent on the incidence of the trait and the heritability on the underlying scale. However, when the incidence was between 25 and 75% and when the heritability in the underlying scale was below 5%, differences were neglectable. The binomial traits used in this study, met these conditions. For the interval traits no problems are to be expected.

The relation between male and female fertility

In chapter 3 the effects of the sire of cow and sire of insemination on 56 days non-return rate and conception rate were analysed by parity. The genetic correlation between the two components changed from negative in heifers to moderately positive in parity three. This change was attributed to the sire of cow component. This suggested that the genetic correlation between fertility in heifers, first parity and older cows differed from unity. The results with regard to the relationships between 56 days non-return rate in heifers and cows (chapter 4), however, indicated genetic correlations very close to one and seem therefore to be conflicting with the results of chapter 3.

Both sets of parameters were estimated with error and it is not clear in advance which parameters are wrong. Therefore eigenvalues of the genetic covariance matrix for 56 days non-return rate were calculated to check the validity of the parameters (Hayes and Hill, 1980). Estimates for the sire of insemination component and the covariance between sire of cow and sire of insemination were based on results from chapter 3, those for the variance and covariance between sire of cow in different paritities on results from chapter 4. Parity 3 was neglected, because the correlations between sire of cow and sire of insemination did hardly change

Table 1. Base matrix of genetic (co)variances (* 10^4). Variances on diagonal, covariances above and genetic correlations below.

trait	traits 1	 2	 3	 4
1. sire of insemination	28.0	-2.0	0.0	16.0
2. sire of cow parity 0	-0.3	1.6	8.0	8.76
3. sire of cow parity 1	0.0	1.0	40.0	43.8
4. sire of cow parity 2	0.44	1.0	1.0	48.0

from parity 2 to 3. Base estimates for the calculation of eigenvalues are given in table I. The genetic correlation between sire of cow components was assumed to be 1.

Because the matrix of genetic (co)variances should be positive definite, all eigenvalues should be positive. These base estimates gave one negative eigenvalue, confirming the observed contradiction. When the genetic correlations between sire of cow component were reduced to about 0.75, all eigenvalues were positive. On the other hand when the genetic correlation between sire of cow components were assumed to be 0.95, the correlation between sire of insemination and sire of cow in parity 0 and 1 and to be at least 0.1 and 0.3, respectively to give a positive definite matrix.

This indicates that even when genetic correlations between non-return rates of cows in different parities is as high as 0.75, the relationship between non-return rates of the sire and those of his progeny may change from negative to positive. When the correlation is close to 1.0, the allowable change is much smaller. Nevertheless, the sire of cow component increased considerably in size with parity. This indicates that different genes are expressed in different parities and therefore the correlation may be less than 1. Effects of milk production and parturition may play a role in this respect.

Evaluation of male fertility

In chapter 2 it was concluded that the routinely evaluation of non-return rates of sires within studs can be improved greatly by a correction for group of descendance, parity and month of insemination. This evaluation which is done every month, should comprise both 28 days and 56 days non-return rate. The first, because it is important to have results available as soon as possible, the latter because this reflects more the differences in conception rate. In addition an annual evaluation should be done to provide information to the dairy farmers. In this analysis the herd effect should also be taken into account. This analysis can be restricted to 56 days non-return rate. It is essential that the insemination results are accounted for sampling effects. In practise non-return rates of sires may be affected by for example differences in culling rate of inseminated cows or subsequent use of natural service after first service. These factors mainly play a role when numbers are small, but their effect is minimised if sampling is accounted for. Differences of interest between sires can only be found when the repeatibility is high, i.e. with large numbers.

Evaluation of female fertility

The measurements used to characterise female fertility concerned the period needed to first insemination (age at first service, calving to first service interval), a measure for conception rate (56 days non-return rate) and period needed for conception (age at conception and days open). Other researchers have used number of inseminations per service period as a measure for conception rate (Janson, 1980a; Haug, 1985). This was not done in this study, mainly to reduce the cost of computation. Measures which may take into account differences in culling rate, were also not considered. The method of evaluation accounted already for selection.

The primary goal of selection for fertility is the improvement of conception rate. The level and variances in measurements of fertility, however, reflect not only biological phenomena, but are also dependent on other conditions, especially the milk production capacity of the cow. Model calculations have shown (Van Arendonk and Dijkhuizen, 1985) that it is profitable to continue inseminating high producers for a longer period than low producers. This results automatically in a positive correlation between calving interval and production capacity, even when the initial correlation between production and fertility is zero. Hansen et al. (1983) found that relationships between production and fertility were less advers when based on part-lactation production than on lactation yield. This influenced especially the trait days open, but to a certain degree also number of inseminations per period. 56 days non-return rate is probably less influenced and is therefore preferable as measure for conception rate.

In addition to conception rate the time of first insemination in cows deserves attention. Selection for reduced age at first service in heifers is not necessary. There seems to be no real biological objections to start inseminating from 15 months onwards under Dutch circumstances, except the development of the heifer itself, which may be considered by the farmer. The interval calving to first service and conception results are about equally correlated to days open. Therefore interval to first service in cows could also be considered as trait for selection in cows. The heritability was slightly higher than that of 56 days non-return rate. However, this may be inflated by differences in production capacity. The main biological cause for long intervals to first service seems to be silent heat or insufficient signs of heat (Zemjanis et al. (1969), cited by O'Farrell (1982)). Therefore heat intensity could be considered instead of interval to first service. These could be scored by technicians, when inseminating cows. A Swedish trial, however indicated very low heritability for the trait measured in this way (Nillsson et al., 1983). Further research on the effects of selection for reduced interval to first service seems necessary, before this trait can be used in selection programs.

In conclusion it seems sufficient to evaluate fertility of cows on the basis of 56 days non-return rate. The impact, however, seems very limited. In The Netherlands progeny testing of young bulls usually results in 75 to 100 daughters with first lactation records. Even when both heifer and first parity results are used, this number is too small to obtain sufficiently high repeatabilities for the evaluation of fertility. Simple index calculations gave repeatabilities of 0.20, 0.25 and 0.36 with 75, 100 and 200 daughters, respectively. As a result differences between sires will be very small. The use of number of inseminations per service period as proposed by Janson (1980b), is no real alternative. He reported that the repeatability based on 120 heifer records and 80 first parity records, would be about 50%, which is still rather low. The consequence of such an evaluation will be that no attention will be paid to fertility of daughters of sires. When results of proven sires are known, much higher repeatabilities can be obtained. These results, however, are known too late to be of interest for selection decisions in current breeding programs. When no evaluation and selection for fertility of cows is carried out, some negative (correlated) respons from selection on milk production is to be expected, due to an antogonistic relation between fertility and milk production. The responses are probably small. Well designed selection experiments for milk production showed no negative respons on fertility (Shanks et al., 1978). Recently Bertrand et al. (1984) reported small adverse effects in later parities and second generation.

Evaluation of herd fertility

In chapter 5 different parameters to monitor dairy herd fertility were studied and their relation to financial loss due to reproductive failure was quantified. Attention was paid to parameters which could be determined as soon as possible in order to be up to date. Losses due to suboptimal calving intervals could be explained very well by three variables: the oestrus index, the average calving to first service interval and 56 days non-return rate. It is suggested to present at least the oestrus index and the interval to first service to the dairy farmer. This requires AI-data and milk recording data to be combined. The purpose of these parameters is solely to monitor herd fertility, not to analyse problem herds. When herds do not meet the standards for these parameters for a long period, veterinary assistance can be called for a detailed analysis of the problems.

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SUMMARY

Fertility is one of the non-yield traits which is of great economic importance in dairy herds. Reduced fertility results in prolonged calving intervals and an increased culling rate. Both are undesirable. Fertility problems account for about 30% of all disposals.

In this thesis it was researched whether the use of routinely collected and processed AI data could be improved both for breeding and management purposes. Much research has been done on breeding aspects of fertility. The main items were summarised in the literature review in chapter one. Three aspects were considered for further research.

Firstly the correction of insemination results of technicians and Friesian bulls in AI was studied. Data were available on 87112 first inseminations by 283 bulls and 37 technicians. The traits studied were 28 and 56 days non-return rates. In the analyses a distinction was made among a monthly and a yearly presentation of results. Differences in age at first service in heifers and calving to first service interval in cows did not affect the ranking of and differences between sires and technicians. The routine monthly evaluation of non-return results of sires required a correction for parity of inseminated animals and month of insemination. Also the percentage Hosltein was of interest. Deviations from the stud average had to be regressed to account for sampling. In obtaining a reliability of 50% for sires at least 300 first inseminations were required. The monthly evaluation of technicians could be based on deviations within studs.

The annual avaluation of both technicians and sires could be further improved if the herd effect was also accounted for. The correlation between solutions corrected for and not corrected for the herd effect was 0.94. After correction for environmental effects the range in solutions for 56 days non-return rate of sires and technicians was about 9%.

Secondly the relationship between insemination results of sires and of their daughters was researched. The success of an insemination is influenced by the quality of the sperm the sire produces (direct effect) as well as the environment in the uterus and the quality of the egg. The latter are affected by the sire indirectly via genes transmitted to his daughters. The traits considered were 56 days non-return rate, conception rate, days open in cows and age at conception in heifers. Traits were analysed by parity. The number of records was 6497, 3704, 6883 and 4711 animals in heifers and cows in parity 1, 2 and 3, respectively.

The relationship between the direct and the indirect effect of the sire changed with the age of the cow: from -0.29 in heifers to 0.59 in parity 3 for 56 days

non-return rate and from -0.74 to 0.48 for conception rate. Changes in days open were smaller and not consistent. It was concluded that use of sires with non-return rates above average would be favourable for the insemination results of older cows, but somewhat adverse on results in heifers.

The direct and indirect effect can be further distinguished among a direct genetic and maternal genetic effect. The first concerns the genetic make up of the embryo, the second the genetic value of the environment in which conception takes place. The observed interaction for the direct and indirect effect with parity number, was also found for the direct genetic and maternal genetic effect. The negative relationships in heifers were even stronger. The cause for this negative relation is not known. The maternal and direct genetic component were about equal for 56 days non-return and conception rate. Days open showed a larger maternal component.

Chapter 4 deals with the relationships between fertility traits in sire progeny groups at different ages. Sire evaluation and selection for fertility based on records of heifers and first parity cows is only effective if the relation with fertility at older ages is high. Insemination results decrease at older ages and culling due to fertility problems increases. The number of records available to study these questions varied between 2307 and 12145 records per parity.

The genetic correlation between age at first insemination in heifers and interval to first service in first parity cows was 0.67, that for age at conception and days open 0.66. The genetic relations between interval to first service in parity 1, 2 and 3 respectively varied from 0.78 to 0.89, that for days open from 0.68 to 1.06. The genetic correlations between 56 days non-return in different parities were above unity.

The results of chapter 3 and 4 seemed to be conflicting. In chapter 3 the relationship between 56 days non-return of the sire and that of his progeny changed with age, whereas in chapter 4 it was found that the genetic relationship between different parities was one. Further analyses as discussed in the general discussion chapter showed that when the genetic correlation between parities was about 0.75, the realised change in the genetic relation between the direct and indirect effect was possible. If the relationship between parities was higher the possible range should be smaller.

In the discussion chapter it is also discussed to what extent selection for daughter fertility would be possible. The trait 56 days non-return rate would be the best to select for, because this is less biased by decisions of dairy farmers. The traits days open and number of inseminations are also affected by the production capacity of the cow. However, current size of progeny groups in first lactation is about

75 to 100 daughters, which is too low to detect sufficiently large differences between daughter groups for non-return rate.

Finally it was studied in which way AI data could be used to monitor herd fertility. Data of 65 herds collected over a period of 3 years, were used. The following herd averages were calculated to characterise herd fertility: interval calving to first service, 56 days non-return rate after first service, percentage reinseminations done in the period 18-24 days after a previous service, fertility status, oestrus index (a measure for the quality of heat detection) and number of inseminations per average cow present in the herd.

These figures were related to loss from prolonged calving interval and loss from culling due to fertility problems. The oestrus index and the fertility status showed the highest correlation with loss from prolonged calving intervals: 0.79 and -0.67, respectively. Interval to first insemination was next with 0.52. Relationships with loss from culling were never significant. The oestrus index, interval calving to first service and 56 days non-return rate were also rather repeatable: 0.63, 0.58 and 0.52, respectively. The repeatability of loss from prolonged calving intervals could be characterised well with three figures. The oestrus index was the most important one, explaining 63% of the differences, the interval to first service explained a further 10% and 56 days non-return rate a further 6%. Loss from culling could not be characterised by figures calculated from AI data. It was concluded that the oestrus index, the interval calving to first service and 56 days non-return rate were to be presented to the farmer as management aids.

SAMENVATTING

Op melkveehouderijbedrijven wordt vruchtbaarheid als een der belangrijkste gebruikseigenschappen beschouwd. Een verminderde vruchtbaarheid leidt tot langere tussenkalftijden en verhoogde afvoer. Dit wordt als ongewenst beschouwd. Bij afvoer worden in 30% van de gevallen vruchtbaarheidsproblemen als reden van afvoer genoemd.

In deze studie is nagegaan op welke wijze KI-gegevens die routinematig verzameld en bewerkt worden, beter dan tot dusver aangewend kunnen worden voor zowel foktechnische als management doeleinden.

De foktechnische aspekten hebben in het onderzoek al veel aandacht gehad. De hoofdpunten hiervan zijn beschreven in hoofdstuk 1. Een drietal aspekten is nader bestudeerd. De beschikbaarheid van gegevens speelde evenzeer een rol bij de keuze.

Allereerst is aandacht besteed aan het opschonen van KI-resultaten van stieren. De inseminatie resultaten van inseminatoren werden tegelijkertijd meegenomen. De KI-verenigingen gebruiken de percentages niet-terug 28 en 56 dagen na 1e inseminatie voor eigen managementdoeleinden, terwijl de veehouders de landelijk gepubliceerde cijfers omtrent het percentage niet-terug 56 dagen van stieren betrekken in de stierenkeus. De cijfers worden momenteel als ruwe maand- en voortschrijdende KI-jaargemiddeldes gepresenteerd. Ze kunnen beïnvloed worden door effekten van jaar, maand en bedrijf van inseminatie. Verder kan de leeftijd van de koe en de periode tussen afkalven en eerste inseminatie een rol spelen. Tenslotte kunnen de resultaten van inseminatoren en stieren elkaar beïnvloeden, doordat sommige inseminatoren meer gebruik maken van betere bevruchtende stieren dan andere. Deze factoren werden onderzocht in een materiaal met ruim 87000 eerste inseminaties, uitgevoerd door 37 inseminatoren op 326 bedrijven.

Bij de analyse werd een onderscheid gemaakt naar de presentatie van maand- en jaarcijfers. De periode afkalven - eerste inseminatie en de leeftijd bij pinken bleken niet van invloed te zijn op de rangorde van en de verschillen tussen zowel stieren als inseminatoren.

De presentatie van de maandcijfers van de stieren kon duidelijk verbeterd worden door rekening te houden met de pariteit van de geïnsemineerde dieren (pinken, 1e kalfs, 2e kalfs etc.) en de maand van inseminatie. Verder bleek het percentage Holsteinbloed van belang. Tenslotte diende het aantal inseminaties waarop het gemiddelde gebaseerd was, in ogenschouw genomen te worden. Om een betrouwbaarheid te verkrijgen van 50% voor stieren waren tenminste 300 eerste inseminaties nodig. De maandcijfers van inseminatoren konden goed vergeleken worden op basis

van ruwe gemiddeldes binnen de KI-vereniging.

De kwaliteit van de jaarcijfers van zowel inseminatoren als stieren kon duidelijk verbeterd worden door tenslotte nog rekening te houden met het bedrijf waarop de inseminatie plaatsvindt. De correlaties tussen de rangorde, gecorrigeerd en niet gecorrigeerd voor bedrijfseffekten, bedroeg 0.94. Na korrektie bleek dat er zowel voor stieren als inseminatoren nog duidelijke verschillen aanwezig waren; voor het percentage niet-terug 56 dagen na eerste inseminatie beide in de orde van grootte van 9%.

In de tweede plaats (hoofdstuk 3) is de relatie tussen inseminatie resultaten van de stier en die van zijn dochters onderzocht. Het resultaat van een inseminatie is zowel afhankelijk van de kwaliteit van het sperma dat de stier levert (direct effekt), als ook van het milieu in de baarmoeder en de kwaliteit van het ei. Deze laatste faktoren worden indirect ook door de stier beïnvloed via de doorgifte van genen aan zijn nakomelingen. De onderzochte kenmerken waren het percentage niet-terug 56 dagen na eerste inseminatie, het percentage concepties (gemeten aan volgende afkalving) en het interval afkalven-conceptie (gustperiode) bij koeien en de leeftijd bij conceptie bij pinken. Deze laatste twee kenmerken worden niet alleen beïnvloed door de bevruchtingsresultaten maar ook door het moment waarop voor de eerste keer met insemineren wordt beginnen. Het materiaal waarin dit onderzocht werd, omvatte 6497, 3704, 6883 en 4711 dieren bij respectievelijk pinken, eerste, tweede en derde kalfs koeien.

Het verband tussen het direkte en indirekte effekt van de stier op de vruchtbaarheid bleek te veranderen met de leeftijd van de koe: voor het percentage niet-terug van -0.29 bij pinken tot 0.59 bij derde kalfs en voor het bevruchtingspercentage van -0.74 tot 0.48. De veranderingen ten aanzien van de gustperiode waren kleiner en niet consistent. Uit de resultaten kon geconcludeerd worden dat het gebruik van goed bevruchtende stieren ietwat nadelig kan uitwerken op de bevruchtingsresultaten van de nakomelingen als pink, maar juist positief op de resultaten bij oudere koeien. Juist bij deze groep koeien zijn de problemen het grootst.

Behalve een onderscheid in het direkte en indirekte effekt van de stier kan ook een onderscheid gemaakt worden in direkt genetische effekten en maternaal genetische effekten. Het eerste heeft betrekking op de genetische samenstelling van het embryo, het tweede op de genetische waarde van het milieu waarin de conceptie plaatsvindt (baarmoeder, eikwaliteit). Deze twee componenten bleken een soortgelijke interactie te vertonen als het direkte en indirekte effekt, zij het dat de genetische correlaties zeer sterk negatief waren bij pinken en ook negatief bij vaarzen wat betreft het percentage niet-terug en bevruchting. De oorzaken hiervan laten zich nog raden. De maternale en direkt genetische component bleken ongeveer even groot voor het percentage niet-terug en het bevruchtingspercentage. Voor de gustperiode was de maternale component groter.

In hoofdstuk 4 is nader onderzocht in welke mate verschillen in vruchtbaarheid tussen dochtergroepen hetzelfde bleven wanneer de dochters ouder werden. Wil een eventuele fokwaardeschatting en selektie op vruchtbaarheid bij melkkoeien effekt hebben dan dient deze bij voorkeur gebaseerd te worden op gegevens verzameld bij pinken en eerste kalfsdieren. In de moderne fokprogramma's vindt de selektie van stieren op melkproduktie al plaats als de 100 dagen en 305 dagen fokwaardes bekend zijn. Daarna worden de beste stieren zeer intensief gebruikt. Vruchtbaarheidsproblemen spelen echter vooral een rol op oudere leeftijd. Een vroegtijdige analyse is dan ook alleen zinvol als de rangorde van stieren op basis van gegevens van pinken en eerste kalfs goed overeenkomt met die van groepen met gegevens van oudere koeien. In de literatuur werden tegenstrijdige resultaten gemeld ten aanzien van de relatie vruchtbaarheid gemeten bij pinken en vaarzen, terwijl er geen informatie was omtrent de verbanden gemeten bij melkgevende koeien. Deze vragen werden onderzocht in een materiaal dat per pariteit varieerde tussen de 2307 en 12145 dieren.

De genetische relatie tussen leeftijd bij eerste inseminatie bij pinken en het interval afkalven eerste inseminatie bij vaarzen was 0.67, die voor leeftijd bij eerste conceptie en gustperiode ("days open") bij eerste kalfs 0.66. De genetische correlaties tussen interval afkalven tot eerste inseminatie bij eerste, tweede en derde kalfs koeien varieerden tussen 0.78 en 0.89, terwijl ze voor de gustperiode varieerden van 0.68 tot 1.06. De genetische correlaties voor het percentage niet-terug 56 dagen na eerste inseminatie op verschillende leeftijden was steeds groter dan 1. Op basis van deze resultaten is geconcludeerd dat de expressie van vruchtbaarheid bij vrouwelijk vee op verschillende leeftijden een goede overeenkomst vertoont.

De resultaten van hoofdstuk 3 en 4 leken in eerste instantie duidelijk tegenstrijdig te zijn. In hoofdstuk 3 werd gevonden dat het verband tussen de percentages niet-terug 56 dagen van de stier en dat van zijn dochters veranderde met de leeftijd van de dochters, terwijl in hoofdstuk 4 gevonden werd dat de rangorde van dochtergroepen op verschillende leeftijden iedentiek was. Een nadere analyse (discussie) liet zien dat er ook bij een hoge overeenkomst in rangorde van dochtergroepen van stieren op verschillende leeftijden, ruimte was voor een verandering in de relatie tussen vruchtbaarheid van de stier en dat van zijn dochters.

In het discussiehoofdstuk is eveneens aandacht besteed aan de vraag in hoeverre selektie op vruchtbaarheid bij dochtergroepen mogelijk is. Het percentage niet-terug zou daarvoor het beste kenmerk zijn, omdat dit het minst beïnvloed wordt door beslissingen van de veehouder. Bij kenmerken als aantal gustdagen en het aantal inseminaties in een bepaalde periode speelt ook het produktievermogen van de koeien een rol. Echter, bij de huidige omvang van dochtergroepen varieërend van 75 tot 100 dochters is de betrouwbaarheid van selektie te laag om voldoende grote verschillen aan het licht te brengen.

Tenslotte is onderzocht op welke wijze de KI-gegevens beter benut kunnen worden voor de karakterisering van de vruchtbaarheidssituatie op de melkveebedrijven zelf (hoofdstuk 5). De gegevens van 65 bedrijven verzameld over een periode van 3 jaar, werden daarvoor geanalyseerd. Bedrijfsgemiddeldes voor een zestal kengetallen werden gebruikt om de situatie te typeren: het interval afkalven tot eerste inseminatie, het percentage niet-terug 56 dagen na eerste inseminatie, het percentage herinseminatie gedaan 18-24 dagen na vorige inseminatie, de fertiliteitsstatus, een maat voor de kwaliteit van bronstdetectie en het aantal inseminaties per gemiddeld aanwezige koe.

Deze kengetallen werden gerelateerd aan de schade tengevolge van een verlengde tussenkalftijd en de schade vanwege afvoer tengevolge van vruchtbaarheidsstoornissen. De oestrus index en de fertiliteitsstatus bleken het sterkst gecorreleerd met de schade van verlengde tussenkalftijd: respectievelijk 0.79 en -0.67, gevolgd door het interval afkalven tot eerste inseminatie (0.52). De relaties met schade vanwege afvoer waren niet significant.

De oestrus index, het interval afkalven tot eerste inseminatie en het percentage niet-terug bleken ook goed herhaalbaar te zijn: respectievelijk 0.63, 0.58 en 0.52. De herhaalbaarheid van schade vanwege verlengde tussenkalftijd was eveneens goed (0.48), die van afvoerschade laag.

Verder is aan de hand van regressie analyse uitgezocht hoe met zo min mogelijk kengetallen een zo goed mogelijke typering kon worden verkregen. De schade van een verlengde tussenkalftijd kon goed geschat worden aan de hand van drie kengetallen. De oestrus index was het belangrijkste kengetal. Het verklaarde 63% van de verschillen. Het interval afkalven tot eerste inseminatie voegde 10% extra toe en het percentage niet-terug tenslotte nog 6%. Door de KI-gegevens aan de melkcontrole gegevens te koppelen kunnen deze kengetallen routinematig ten behoeve van het bedrijfsbeheer berekend worden.

Curriculum vitae

Jan Jansen werd geboren op 29 juli 1954 te Wezep, waar hij op een melkveebedrijf opgroeide. In 1972 behaalde hij zijn diploma gymnasium-B aan het Carolus Clusius College te Zwolle. Zijn studie aan de Landbouwhogeschool werd in 1979 met lof afgesloten. Het doctoraalexamen in de Zoötechniek omvatte het hoofdvak de Veeteelt en de bijvakken de Gezondheids- en Ziekteleer der Huisdieren, de Erfelijkheidsleer en de Industriële Bedrijfskunde. Na zijn afstuderen werd hij aangesteld als wetenschappelijk medewerker bij de vakgroep Veefokkerij. Sinds 1 december 1985 is hij als Technisch Direkteur verbonden aan het Fries Rundvee Syndicaat te Leeuwarden, speciaal belast met fokkerijtechniek en automatisering.