DYSTOCIA IN DAIRY CATTLE BREEDING

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A. Meijering

DYSTOCIA IN DAIRY CATTLE BREEDING

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C.C. Oosterlee,
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Omslagontwerp: Peter Bergström

Meijering, A., 1986. Dystocia in dairy cattle breeding
(Geboortemoeilijkheden in de melkveefokkerij)

aan mijn ouders
aan Saskia en Linda

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STELLINGEN

1. Benadering van de kategorische gegevens over het geboorteverloop met een zogenaamd drempelmodel is niet alleen op statistische maar ook op biologische gronden verdedigbaar.

   Dit proefschrift.

2. Het aanwezig zijn van een negatieve korrelatie tussen de direkte en de maternale genetische component ten aanzien van het geboorteverloop is op zich onvoldoende om te veronderstellen dat de eerste partus bij dochters van zogenaamde pinkenstieren moeilijker zal verlopen dan gemiddeld.

   Dit proefschrift.

3. De konklusie van Berger en Freeman dat de precisie van fokwaardeschatting voor geboorteverloop met een BLUP-model wordt verhoogd door vervanging van homogene door heterogene restvariantie is onjuist.

   Berger, P.J. en Freeman, A.E., 1978. Prediction of sire merit for calving difficulty. Journal of Dairy Science 61: 1146-1150.

   Dit proefschrift.

4. Het Optimale Draagtijden Percentage, zoals gedefiniëerd door Remmen, is geen optimaal kriterium bij de selektie van KI-stieren voor geboortemoeilijkheden.

   Remmen, J.W.A, 1976. Een onderzoek naar mogelijkheden om perinatale sterfte bij het rund te beperken. Proefschrift Rijksuniversiteit Utrecht.

5. Het kort voor de partus verplaatsen van vaarzen naar een afkalfstal kan het

partusverloop in negatieve zin beïnvloeden en dient daarom te worden ontraden.

Dufty, J.H., 1981. The influences of various degrees of confinement and supervision on the incidence of dystocia and stillbirth in Hereford heifers. New Zealand Veterinary Journal 29: 44-48.

6. Veler visie op de toekomstmogelijkheden van het MRY-ras getuigt van zwartwit denken.

7. Prijsdifferentiatie van nuchtere kalveren op basis van een fokwaarde voor vleesproduktie-eigenschappen van de vader zou meer bijdragen aan de handhaving van de vleesproduktiegeschiktheid van de rundveestapel dan differentiatie op grond van kleur of ras.

8. De noodzaak tot kontrole van de afstamming via bloedgroepenonderzoek neemt toe met de waarde van het individu in de fokkerij.

9. De wenselijk te achten aktieve participatie van statistici in onderzoekprojekten impliceert dat de statisticus bij voorkeur niet moet worden geconsulteerd.

10. Bij de popularisering van resultaten van wetenschappelijk onderzoek op het terrein van de rundveeverbetering wordt de specifieke kennis van de voorlichtingsdienst onvoldoende benut.

11. De dikwijls nostalgische opdruk van melkkartons doet twijfelen aan het vermogen van de witte motor.

Proefschrift van A. MEIJERING
Dystocia in dairy cattle breeding

Wageningen, 14 mei 1986

Voorwoord

(preface)

Rundveefokkerij, toegepast dan wel experimenteel, is een zaak van lange adem. Het onderzoekprojekt dat tot dit proefschrift heeft geleid, heeft dan ook vele jaren gevergd. Eenieder die in deze periode op enigerlei wijze heeft bijgedragen aan de uitvoering van dit projekt of aan de totstandkoming van dit proefschrift wil ik daarvoor graag danken.

Het onderzoek werd voor het overgrote deel uitgevoerd bij het Instituut voor Veeteeltkundig Onderzoek "Schoonoord" te Zeist. De direktie van het instituut, Dr. Watze Sybesma en Ir. Durk Minkema, ben ik zeer erkentelijk voor de mij geboden mogelijkheden: met name de vrijheid die me gelaten is om het projekt grotendeels naar eigen inzicht in te vullen heb ik zeer gewaardeerd. De leden en ex-leden van de Werkgroep Fokkerij, waartoe ook mijn co-promotor Dr.Ir. Pim Brascamp behoort, wil ik graag dank zeggen voor de stimulerende diskussies en voor de waardevolle suggesties ten aanzien van de manuskripten. Voor de statistische ondersteuning ben ik dank verschuldigd aan de medewerkers van IWIS-TNO, Drs. Jos Jansen, Drs. Bas Engel en Wim Buist. Met name de, soms filosofisch getinte, diskussies over de statistische methodiek met jou, Bas, heb ik zeer gewaardeerd. Ing. Peter van Eldik en Ing. Hans Kooper ben ik erkentelijk voor de steun bij de dataverwerking. In de persoon van Elly Kroeze wil ik de dames bedanken die het typewerk verzorgden. Het tekenwerk was bij Henk de Vries steeds in vertrouwde handen.

Het dierexperimentele gedeelte van het onderzoek werd uitgevoerd op proefbedrijf 't Gen te Lelystad. Graag dank ik alle medewerkers van dit bedrijf, in het bijzonder Jaap Kikstra en Ing. Dick v.d. Ploeg, voor hun inzet en belangstelling.

Een bijzonder woord van dank wil ik richten aan Albert Postma. Door jouw inzet, organisatievermogen en alertheid, Albert, is de afstand Zeist-Lelystad op geen enkele wijze belemmerend gebleken.

Mijn promotor, Prof.Dr.Ir. R.D. Politiek wil ik bedanken voor de voortdurende belangstelling bij de uitvoering van het onderzoek en voor het geloof in de foktechnische mogelijkheden van een niet-fokkerijstudent.

A relatively small but very significant part of the research underlying this thesis was performed in the Department of Animal Science, University of Illinois, Urbana, USA, in cooperation with Dr. Daniel Gianola. Dan, the contribution by you and your students to this thesis, and your hospitality during our stay in Urbana, are most sincerely appreciated.

Contents

INTRODUCTION

Dystocia (calving difficulty), is an undesirable phenomenon in cattle production. When the expulsion of a calf is obstructed, the well-being of both the calf and its dam are endangered. Assistance by the herdsman or a specialist, usually a veterinary surgeon, is required then in order to limit the damage. Herdsmen are well-aware of the risks involved in a parturition and they tend to supervise, or to lend minor assistance to, every cow in labour. Termination of a difficult calving, even though the aid of a specialist may not yet be necessary, will demand more time and manpower which has to be appreciated negatively. Concurrently the risk of damage to the calf, its dam or both will increase. Calling in the aid of a veterinary surgeon, if done in good time, may limit the risk but it involves expenses. At worst, the calf can only be delivered by ceasearean section or fetotomy.

The risk of a difficult calving with respect to the well-being of the calf is clearly illustrated by the increased stillbirth rates at difficult parturitions found in numerous studies. The possible damage to the dam is not as well documented. There is evidence however, of a lower milk yield and a reduced fertility as a consequence of a difficult parturition. Besides, the culling rate among cows with calving difficulty tends to be above average.

From field data recorded in the early seventies the frequency of dystocia in purebred Dutch Friesians and Meuse-Rhine-Yssel cattle was estimated at 15-17% at first calving and at 5-6% at second and following calvings (Meijering, 1980). Corresponding stillbirth rates were 9-12% at first and 2.5-3.5% at second and following calvings. These figures clearly express the size of the problem. Moreover, the effect of parity is evident: cows are subject to dystocia at first calving in particular.

Studies in the sixties and seventies identified a number of additional factors with an effect on the incidence of dystocia and stillbirth. These are reviewed in chapter 1. In view of the possibilities to reduce the incidence of dystocia and stillbirth it is of major importance that these traits were found to be subject to genetic influences. Already in 1963 Van Dieten showed that both the sire of the calf and the sire of the cow contribute to the probability of dystocia and stillbirth. He introduced the so-called heifer-bull-programme which involves testing of young bulls for the sire-of-calf effect and recommending bulls with low incidences of dystocia and stillbirth among their progeny for heifer matings. Subsequently, this programme was gradually adopted by the Dutch AI organisations. Philipssons (1976) thesis on calving difficulty, stillbirth and associated factors in Swedish cattle breeds, which includes the estimation of direct and maternal genetic parameters, lead to a growing interest in calving traits among animal breeders. In 1977 the Research Institute for Animal Production "Schoonoord" initiated a project on dystocia with emphasis on the genetic aspects, which resulted in this thesis.

The first main line in the project was the optimization of the heifer-bull-programme of which the optimization of sire evaluation was an important aspect. From the review of literature it became evident that the method of sire evaluation considered to be optimal for continuous traits, i.e. Best Linear Unbiased Prediction (BLUP), has to be viewed as suboptimal for dystocia and stillbirth since the data are categorical and do not follow the normal distribution. In chapter 2 the results of a comparison with simulated data between BLUP and a theoretically more appealing nonlinear procedure, suggested by Gianola and Foulley (1983), are presented. Chapter 3 gives the results of a comparison between "standard" BLUP and a modification proposed by Berger and Freeman (1978) also with simulated data. In chapter 4 BLUP and the nonlinear method of Gianola and Foulley (1983) are compared with field data from the Dutch birth recording programme.

The second main line in the project was a study of the nature and size of maternal genetic effects and direct-maternal-interaction. Maternal genetic effects are effects of the genotype of the dam which are expressed in traits of the dam, e.g. pelvic dimensions. The direct genetic effect refers to the influence of the genotype of the calf. More information on these topics was felt necessary for the construction of an optimal sire selection programme for dystocia and stillbirth. Chapter 5 refers to a study into the association between ease of calving and a number of, mainly morphologic, dam traits. In chapter 6 the responses found in a sire-selection-trial for dystocia are reported.

Results from the studies mentioned and from recently reported studies by others were integrated in a comparison of the monetary returns from three sire-selection-schemes for calving traits which constitutes the final chapter.

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Part I

REVIEW OF LITERATURE

Chapter 1

Dystocia and stillbirth in cattle
- a review of causes, relations and implications

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DYSTOCIA AND STILLBIRTH IN CATTLE — A REVIEW OF CAUSES, RELATIONS AND IMPLICATIONS

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ABSTRACT

Meijering, A., 1984. Dystocia and stillbirth in cattle — a review of causes, relations and implications. *Livest. Prod. Sci.*, 11: 143—177.

Research into calving difficulty (dystocia) and stillbirth in both dairy and beef cattle, as reported during the last two decades, is reviewed with emphasis on causes and effects. The present concept of hormonal control of parturition is briefly outlined. Causes of dystocia and stillbirth and their relative contributions to the cases observed in field data, veterinary practise and obstetric clinics are discussed. Direct (loss of calf, death of dam, labour, veterinary assistance) and longer term (culling rate, milk yield, fertility) costs are summarized. After going briefly into difficulties encountered in heritability and correlation estimates and their interpretation when categorical data are involved, phenotypic relationships between calving performance and calf traits, dam traits and gestation length are dealt with extensively. The effects of non-genetic factors (parity, sex of calf, age at first calving, season, level of nutrition during gestation) and their supposed modes of action are reviewed. The genetic model for calving traits is outlined and the estimates for the components suggested to be involved (direct, maternal, direct—maternal interaction) are summarized. Three topics in sire evaluation for the direct genetic component are discussed extensively, viz. the possible contribution of traits of the sire (birth weight, gestation period, body dimensions, performance test results), the alternatives in choice of mates in progeny testing, and methods of evaluation (BLUP, non-linear models). Finally, alternative strategies in selection against dystocia are compared.

INTRODUCTION

In the last two decades research has shown great interest in parturition of cattle and, particularly, in calving complications. Since the spade-work by Van Dieten (1963), a large number of papers have appeared, by veterinarians as well as agronomists, dealing with frequencies of calving difficulties and stillbirths. The increasing availability of advanced computer systems has facilitated the analysis of large data sets, consequently enabling an accurate valuation of factors affecting these frequencies. In recent years attention in this area has shifted more and more to the development and improvement of breeding strategies to reduce calving difficulty (dystocia) and stillbirth rates.

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Meanwhile, research efforts in the fields of endocrinology and physiology have led to a better understanding of the parturition process itself, and comparative morphological studies have yielded indications about the basic causes of dystocic calvings.

In the present paper research with respect to calving difficulty and stillbirth reported during the last twenty years will be reviewed in order to present a survey of the actual state of knowledge and to indicate possible voids, as a point of departure for additional research. Emphasis will be upon causes and effects. No survey of levels of dystocia and stillbirth incidence, as reported for different breeds or breedcrosses, will be presented. These figures can be found elsewhere (e.g. Philipsson, 1976a; Menissier and Foulley, 1979; Philipsson et al., 1979; Smidt and Huth, 1979). Dystocia in U.S. beef cattle has been previously reviewed by Price and Wiltbank (1978a). Earlier reviews with respect to dystocia and stillbirth in European cattle breeds can be found in the proceedings of a seminar on calving problems and early viability of the calf, held at Freising (Federal Republic of Germany) in 1977 (Hoffmann et al., 1979).

PRESENT CONCEPT OF PARTURITION CONTROL

Parturition in cattle is a complicated physiological process that still needs elucidation in important aspects. It is generally accepted that the onset of parturition is initiated by the fetus. A concept has been developed, partly based on studies in sheep and goats, in which the first sign of parturition (an increasing activity of the fetal pituitary—adrenal axis) is followed by a cascade of hormone action, involving fetal corticosteroids, placental estrogens and prostaglandins, and oxytocin (Thorburn et al., 1977; Schulz et al., 1979; Thorburn, 1979). The primary trigger to this process is, however, not exactly known. Schulz et al. (1979) suggested that the onset of parturition might be associated with the degree of maturation of the fetal central nervous system.

Features observable in the preparative stage of parturition, such as the increasing elasticity and relaxation of the cervix, vagina, vulva and pelvic ligaments, are ascribed to estrogen action (Schulz et al., 1979). Cervical dilatation is accomplished by uterine contractions, invoked by the synergistic action of prostaglandins, oxytocin and mechanical stimuli, and, as parturition progresses, by the stretching influence exerted by the entering fetus (Rüsse, 1965). Finally, powerful uterine contractions, supported by abdominal straining bouts, achieve the expulsion of the fetus.

In normal circumstances this complicated process should terminate without human interference being required, leaving a healthy cow with a vital calf. In reality, however, a significant proportion of calvings is assisted to a major degree and/or yields a stillborn calf, as shown in the surveys referred to in the introduction.

DEFINITIONS AND IMPORTANT CAUSES OF STILLBIRTH AND DYSTOCIA

Stillbirth commonly includes calf mortality shortly before, during and within a limited period after parturition. In order to discriminate mortality associated with parturition from abortions a minimum limit is often put upon gestation length. To discriminate it from postnatal mortality due to infectious and/or digestive diseases, the postnatal period considered is commonly restricted to 24 or 48 hours. This procedure, suggested by Van Dieten (1963), was later adopted as a general guideline by an EC/EAAP working group on sire evaluation for dystocia and stillbirth (Philipsson et al., 1979). In some papers longer postnatal periods have been considered; these will be indicated when they are referred to.

Cases of stillbirth may roughly be divided into those associated with difficulties at calving and those occurring in deliveries considered normal. As to the first group, examination of blood gas values of newborn calves has shown that a prolonged parturition or a delivery terminated by forced traction may result in a severe acidosis due to oxygen deprivation (Moore, 1969; Massip, 1980; Eigenmann, 1981). As blood pH drops, first vitality is reduced, subsequently vital organs (e.g., the brain) are damaged and ultimately the fetus dies (Naaktgeboren and Bontekoe, 1976; Walser and Maurer-Schweizer, 1979; Eigenmann et al., 1981). Though this may be the most common course in stillbirth cases associated with dystocia, the definition of stillbirth allows inclusion of cases where a fetus, dead before term, is the cause of dystocia, as reported by Cloppenburg (1966) and Sloss (1970) for 6—15% of their difficult calvings. Evidence is abundant that stillbirth incidence, and even incidence of calf mortality up to one month after calving (Dreyer and Leipnitz, 1971; Dreyer, 1973), is much higher when parturition is judged difficult (e.g., Van Dieten, 1963; Cloppenburg, 1966; Laster and Gregory, 1973). Nevertheless it should be stressed that a major proportion of stillborn calves results from calvings reported to be normal: 40—60% in Swedish (Philipsson, 1976a) and Dutch (Meijering and Van Eldik, 1981) birth recording data. Other factors are therefore important as well. Little is known about these factors however. Increased stillbirth incidence among twin calves not accompanied by a concurrent rise in dystocia incidence (e.g., Cloppenburg, 1966; Philipsson, 1976a; Remmen, 1976), suggest that at least some of these cases may be due to a reduction in the vitality of calves with a low birth weight born after a relatively short gestation period. Congenital defects seem to be of little importance (Lindhé, 1966; Dreyer and Leipnitz, 1971; Lindhé, 1974).

A case of dystocia may broadly be defined as a delivery requiring more assistance than desirable. Such a definition, however, leaves plenty of room for subjective interpretation, which is particularly undesirable in field data collection. Scoring procedures for calving performance have therefore been developed. Although the number of categories may vary, higher scores commonly reflect a higher amount of assistance, expressed in number of men or amount of mechanical pulling force, while the highest scores are assigned to veterinarily assisted deliveries (including caesareans). Scores may be presented as such, or be rearranged in dystocic and non-dystocic calvings, the truncation point being dependent on habit or local conditions. Under range conditions for instance, any assistance may be undesirable and regarded as dystocia (e.g., Bellows et al., 1971; Brinks et al., 1973; Burfening et al., 1978a, b, c), while under conditions of more intensive management, assistance by two men may still be regarded as normal (e.g., Hässig and Schlote, 1979). Estimates of dystocia incidence are therefore poorly comparable.

Dystocia may arise from a number of phenomena, those most frequently met being summarized in Table I. Due to different definitions of dystocia and methods of data collection, the figures stated are not easily comparable, yet some general conclusions may be drawn. Obstruction of calf expulsion because of calf size or pelvic dimensions of dam, generally summarized as feto-pelvic incompatibility (FPI), seems to be the most important single cause of dystocia (e.g., Dreyer, 1965; Sloss and Johnston, 1967; Baier et al., 1973) especially in first calf heifers (Friedli, 1965; Williams, 1968; Konermann et al., 1969) and maybe even more so in beef than in dairy breeds (Sloss, 1970; Menissier, 1979; Menissier et al., 1981). The contribution of this phenomenon to severe dystocia cases in dairy heifers, as encountered in obstetric clinics, is striking (Konermann et al., 1969; Baier et al., 1973). The association between dystocia and size and dimensions of calf and dam will be discussed extensively in a later section.

Posterior or abnormal presentation of the calf, though being observed in only 2—6% of all calvings (Philipsson, 1976a; Price and Wiltbank, 1978b; Meijering and Van Eldik, 1981), are held responsible for 20—40% of the dystocia cases recorded by inquiry (Dreyer, 1965; Cloppenburg, 1966; Philipsson, 1976a) or met in veterinary practise (Friedli, 1965; Sloss and Johnston, 1967). In reports from obstetric clinics (Konermann et al., 1969; Baier et al., 1973), the contribution of deviating presentations is surprisingly low. The fact that this cause of dystocia is relatively more frequently observed in older cows than in heifers (Cloppenburg, 1966; Baier et al., 1973; Philipsson, 1976a) may be attributable to the higher rate of FPI in the latter group.

Weak labour can be the cause as well as a consequence of a difficult calving (Friedli, 1965; Philipsson, 1976a). As most figures reported are not based on observations of entire parturitions, they may poorly indicate the proportion of dystocia cases primarily invoked by weak labour. Primary weak labour is reported to be most frequent in older cows (Friedli, 1965; Sloss, 1970), possibly often associated with milk fever (Sloss, 1970). Insufficient dilatation of the cervix and uterine torsion may contribute significantly to the incidence of severe dystocia, especially in older cows (Friedli, 1965; Konermann et al., 1969; Baier et al., 1973). The relative contribution of these causes is probably low in data collected by inquiry.

TABLE I

Important causes of dystocia and their relative contribution to dystocia cases observed

Author(s)	Dystocia definition	Method of data collection	Data from:		Relative frequencies				
			Heifers	Cows	Feto-pelvic incompatibility	Posterior and abnormal presentation	Weak labour	Insufficient dilatation of cervix	Uterine torsion
Dreyer (1965)	>2 men	Inquiry	+	+	57.3	34.4	1.1		
Friedli (1965)	Vet. assist.	Vet. practise	+				0.0		5.7
Friedli (1965)	Vet. assist.	Vet. practise	+	+	36.8	38.4	7.5		12.5
Cloppenburg (1966)	>2 men	Inquiry	+			21.1			
Cloppenburg (1966)	>2 men	Inquiry		+		33.3			
Sloss and Johnston* (1967)	Vet. assist.	Vet. practise	+	+	46.0	26.0	5.4	9.0	
Konermann et al. (1969)	Vet. assist.	Obstetric clinic	+		73.4	1.7		14.4	6.3
Konermann et al. (1969)	Vet. assist.	Obstetric clinic		+	21.2	4.6		32.3	23.1
Sloss** (1970)	Vet. assist.	Vet. practise	+	+	29.9	24.6			
Baier et al. (1973)	Vet. assist.	Obstetric clinic	+		86.3	2.1		2.4	4.6
Baier et al. (1973)	Vet. assist.	Obstetric clinic		+	36.7	13.1		17.6	21.5
Philipsson (1976a)	>1 man	Inquiry	+			25.0			
Philipsson (1976a)	>1 man	Inquiry		+		50.0			
Price and Wiltbank* (1978b)	Forced traction	Exp. station	+			11.6			
Liboriussen (1979)	>2 men	Inquiry		+		16.1			

*Beef breeds.
**Partly beef breeds.

Finally, two infrequently reported phenomena should be mentioned. First, two papers by Dufty (1972, 1981) reported a dramatic increase in the incidence of dystocia, associated with vulval constriction and irregular labour, when Hereford heifers, normally kept under Australian range conditions, were confined and intensively observed. This phenomenon shows similarity with the effect of stress on parturition of ewes, as reported by Bontekoe et al. (1977), and seems to point to the beneficial effect of a stress-free, familiar environment on ease of calving. Secondly, O'Brien and Stott (1977), Osinga (1978) and Erb et al. (1981) reported a relationship between estrogen levels in blood or urine of the dam two to three weeks before calving and the occurrence of dystocia, low estrogen levels being associated with difficult calvings. The biological nature of this relationship and the contribution of this phenomenon to the dystocia frequencies observed are unknown.

Summarizing this section, 40—60% of stillbirth cases as observed in data collected by inquiry are associated with dystocia, the factors responsible for the other stillbirths being largely unknown. Dystocia in heifers seems to be mainly caused by feto-pelvic incompatibility (FPI), with deviations in presentation accounting for a second substantial part. Other phenomena, like weak labour, uterine torsion or insufficient cervical dilatation, may cause severe dystocia, their contribution to the occurrence of calving difficulty being more significant in older cows, where feto-pelvic incompatibility is less frequently met than in heifers.

ECONOMIC CONSEQUENCES

Only a few attempts have been made to obtain a complete quantification of the economic consequences of dystocia and stillbirth, probably because the consequences are diverse in nature. The most elaborate estimation, pertaining to dairy cattle, was presented by Philipsson (1976e). Obvious sources of costs, directly associated with calving problems, are loss of calf, death of dam, extra labour required from the farmer and veterinary assistance (Philipsson, 1976e; Meijering, 1980a). In Philipsson's estimation about half of the costs were due to loss of calf, stressing both the economic importance of stillbirth within the dystocia—stillbirth complex, and the dependency of the outcome of any estimation upon the value of newborn calves. Cows may occasionally have to be emergency-slaughtered when calving has been extremely difficult. Philipsson (1976e) reported a 3.5% emergency slaughter rate among Friesian heifers with dystocic calvings and a 6.2% rate among those giving birth to a stillborn calf. Friedli (1965) presented a figure of 2.9% for Fleckvieh cows requiring veterinary assistance at calving. The frequency of veterinary assistance at dystocic calvings was assessed at 20% in Friesian heifers by Philipsson (1976e) and at 20—30% in second calf Dutch Friesian and Red and White cows by Meijering and Van Eldik (1981). Cost of veterinary assistance depends on the kind of obstetric aid given, which is in turn dependent on the severity of the dystocia (Meijering, 1980a).

A number of authors have found unfavourable longer-term effects of calving problems. Calves, if not stillborn, may have suffered seriously from a dystocic parturition and may consequently be less vital, resulting in a higher mortality rate or retarded growth during the rearing period (Dreyer and Leipnitz, 1971; Dreyer, 1973; Schulz et al., 1979). Furthermore, the culling rate among cows is higher when calving has been difficult or when the calf was stillborn (Van Dieten, 1963; Philipsson, 1976e; Christensen and Pedersen, 1978; Gaillard, 1980). Increases in culling rate reported vary from 2% (Gaillard, 1980) to 30% (Christensen and Pedersen, 1978). Higher culling rates among these cows may be due to a number of factors, such as calving lesions, depressed fertility, disappointing milk yield or concern about repeat calving problems. Because of more frequent culling it is difficult to assess to what extent fertility and milk yield are affected by calving problems, as pointed out by Philipsson (1976e). Most authors (Konermann et al., 1969; Hansen, 1975b; Vogt-Rohlf and Lederer, 1975) found the effects of dystocia on first lactation milk and butterfat yield to be negligible, but they did not include extended lactations of culled heifers. Philipsson (1976e), although including truncated production records, obtained a similar result. Christensen and Pedersen (1978), on the other hand, reported a significant depressive effect of dystocia on butterfat yield over the first two months of lactation (~10%), while the drop in the 305-day lactation yield was less pronounced (~5%). This suggests that production might recover to a normal level after the first few months of lactation.

As to fertility, the first effect encountered is that the incidence of retained placenta tends to be doubled in heifers and manifolded in older cows when calves are stillborn (e.g., Van Dieten, 1963; Brands, 1966; Christensen and Pedersen, 1978). Negative effects of dystocia alone in this respect seem to be less pronounced or absent (Van Dieten, 1963; Brands, 1966; Christensen and Pedersen, 1978), unless parturition is terminated by very heavy traction or caesarean section (Konermann et al., 1969; Baier et al., 1973; Remmen, 1976). There is good agreement that average insemination results are negatively affected by dystocia as well as by stillbirth (e.g., Van Dieten, 1963; Laster et al., 1973; Hansen, 1975b; Gaillard, 1980). The effect of dystocia on non-return rate after first insemination is likely to depend on degree of difficulty and is reported to vary (in absolute terms) from 5 to 15% when calving was terminated by moderate traction up to 25 to 45% after caesareans (Menissier, 1975b; Gaillard, 1980). Van Dieten (1963) and Philipsson (1976e) reported a 15% lower average non-return rate after first insemination when stillbirth had occurred, while Van Dieten (1963) found a similar drop in results for second and third insemination.

Covering most of the sources of costs discussed, and allowing for a 0.5% rise in stillbirth incidence per percentage point increase in dystocia level and a calf price of 460 Swedish Crowns, Philipsson (1976e) assessed the costs of the dystocia–stillbirth complex at 445 Swedish Crowns per case of dystocia. As stressed before, the outcome of this and any other estimation is particularly sensitive to the assumption made for calf price. In other terms, Philipsson's estimation comes down to 215 Swedish Crowns + half of the calf price.

CATEGORICAL TRAITS

Before discussing traits related to and factors affecting levels of dystocia and stillbirth, some difficulties encountered in genetic—statistical analysis of these traits should be touched upon. Calving performance and stillbirth are scored in two (percentage) or more, but always a limited number of categories, as pointed out in a former section. As the binomial or multinomial distributions then involved imply variance to be dependent on the mean, the basic requirements for the application of analysis of variance in linear models (i.e., normality, equal subclass error variance and additivity of effects) are violated. This problem might be met by appropriate transformation of data or subclass frequencies. After transformation, parameter estimates appear to differ only slightly from estimates on raw data (Sagebiel et al., 1969; Rönningen, 1975; Tong et al., 1977; Gianola, 1979a). Least squares analysis is therefore commonly applied to raw calving performance and stillbirth data, accepting the decreased sensitivity of statistical tests and the non-minimum error variance on the estimators (e.g., Philipsson, 1976b,c; Hässig and Schlote, 1979). Alternatively, an attempt to accommodate for heterogeneous subclass error variances by generalized least squares procedures can be made (Pollak, 1975; Pollak and Freeman, 1976). It should however be pointed out that the development of log—linear and non-linear models has received increased attention recently (Gianola, 1979a, 1980a, b; Gianola and Foulley, 1982) in view of an optimal genetic evaluation for categorical traits. This development may yield procedures applicable in the analysis of large data sets in the near future.

Although the categorical nature of dystocia and stillbirth implies discontinuous variation, quantitative inheritance is assumed (e.g., Belic and Menissier, 1968; Auran, 1972). Therefore, in concurrence with the concept originally adopted for viability of poultry (Robertson and Lerner, 1949; Dempster and Lerner, 1950), a non-observable underlying normal distribution of environmentally and genetically influenced liability values is assumed, which responds in the observable scale by one or more thresholds (e.g., Falconer, 1960). Though, given this concept, a number of objections can be raised against genetic evaluation by linear models in the observable scale, as discussed by Gianola (1980a), further discussion here will be limited to the impact on heritability and correlation estimates. Heritability estimates for categorical data are dependent on incidence in the case of an all-or-none trait like stillbirth (e.g., Dempster and Lerner, 1950; Hill, 1977; Hill and Smith, 1977) and both on category frequencies and category weights in the case of polytomous traits like calving performance score (Tong et al., 1977; Gianola, 1979b, 1980a, 1982). In both cases 'true' heritability (if this were estimable in the underlying continuous scale) would be more or less seriously underestimated. 'True' heritability can be approximated from the estimates in the observable scale by the formula (Gianola, 1979b, 1980a, 1982)

$$h_n^2 = h^2{}_d/\alpha$$

$$\text{in which } \alpha = \left[\sum_{i=1}^{m-1} z_i\,(a_{i+1} - a_i)\right]^2 \Big/ \left[\sum_{i=1}^{m} a_i^2 p_i - \Big(\sum_{i=1}^{m} a_i p_i\Big)^2\right] \qquad (1)$$

h_n^2 = heritability in the underlying scale
h_d^2 = heritability in the observable scale
z_i = ordinate of the standard normal density function at point t_i corresponding to the threshold between categories i and $i + 1$
a_i = weight assigned to category i
p_i = frequency observed in category i

If $|\,a_{i+1} - a_i\,| = 1$, (1) reduces to (Vinson et al., 1976; Jansen, 1980)

$$\alpha = \Big(\sum_{i=1}^{m-1} z_i\Big)^2 \Big/ \left[\sum_{i=1}^{m} a_i^2 p_i - \Big(\sum_{i=1}^{m} a_i p_i\Big)^2\right] \qquad (2)$$

In the case of all-or-none traits, (2) simplifies to the expression derived by Robertson in an appendix to the paper by Dempster and Lerner (1950)

$$\alpha = z^2/p\,(1-p) \qquad (3)$$

By means of simulation, Van Vleck (1972) and Olausson and Rönningen (1975) showed that (3) yields acceptable approximations over a wide range of values for h_d^2 and p, the bias becoming large however at high heritabilities and/or either low or high incidence levels. Expressions (1) and (2) have not been tested by simulation, but may behave in a similar fashion with respect to heritability and degree of skewness. Expressions (1)—(3) do not only yield a fair approximation of 'true' heritability, comparable with estimates for continuous traits, they also provide a tool for indirect comparison of heritabilities estimated in differently distributed or scored categorical data sets, as met in the literature. Examples of the effect of recomputation will be presented.

Phenotypic correlation coefficients involving categorical traits may also be seriously underestimated, as shown in simulation studies by Olausson and Rönningen (1975) and Mao (1976). Vinson et al. (1976), Jansen (1980) and Gianola (1982) showed that phenotypic correlation coefficients can be made approximately correspondent with the underlying continuous scale(s) by

$$r_n = r_d/\alpha^{\frac{1}{2}}$$

in the case of one categorical trait and

$$r_n = r_d/\alpha_1^{\frac{1}{2}} \cdot \alpha_2^{\frac{1}{2}}$$

when both traits are categorial, where r_n = the phenotypic correlation coefficient corresponding to the underlying scale(s) and r_d = the phenotypic correlation coefficient estimated in the observed scale(s)
$\alpha, \alpha_1, \alpha_2$ = as in (1), (2) or (3).

Examples of recomputation of correlation coefficients will be given.

Both simulation work (Olausson and Rönnningen, 1975; Mao, 1976) and theory (Vinson et al., 1976; Jansen, 1980; Gianola, 1982) suggest that genetic correlation coefficients involving categorical traits are unbiased and, consequently, do not need transformation.

PHENOTYPIC EFFECTS OF SIZE AND SHAPE OF THE CALF

From the review of causes of dystocia, it was concluded that feto-pelvic incompatibility (FPI) is likely to be the main reason for calving difficulty in heifers, and an important cause in older cows too. FPI may result from an oversized calf, a dam with pelvic dimensions below average, or both (Friedli, 1965; Williams, 1968). Calf size is commonly recorded as birth weight. Whenever birth weight was examined as a source of variance in level of dystocia, it appeared to be highly significant, both in heifers and in cows (e.g., Dreyer, 1965; Laster and Gregory, 1973; Notter et al., 1978). The same applies to the level of stillbirths, though in this case the effect in older cows may be less pronounced (Van Dieten, 1963; Cloppenburg, 1966; Philipsson, 1976c; Remmen, 1976). The effect of birth weight has to be evaluated within parity groups, as parity affects birth weight and dystocia or stillbirth level inversely, heifers yielding calves with lower birth weights than older cows, but showing higher rates of dystocia and stillbirth incidence (e.g., Philipsson, 1976b; Burfening et al., 1978c; Gaillard, 1980). The relattionship between birth weight and dystocia incidence was found to be non-linear (e.g., Menissier, 1975b; Philipsson, 1976c; Burfening et al., 1978a), the frequency of dystocia rising sharply when birth weight exceeds a threshold value, though deviation from linearity may sometimes be small in heifers (Cloppenburg, 1966; Notter et al., 1978; Short et al., 1979). Important factors determining the position of the threshold are breed and parity of dam (Menissier, 1975b). The position of the threshold will also depend on the definition of dystocia, as the frequency of more serious cases (e.g., caesareans) starts to rise at higher birth weights than that of less severe cases (Burfening et al., 1978a; Meijering, 1980a). A similar threshold, probably associated with the one for dystocia, can be observed for stillbirth incidence (e.g., Philipsson, 1976c; Remmen, 1976; Notter et al., 1978). In addition, Pijnenburg (1974), Remmen (1976) and Notter et al. (1978) observed an increase in stillbirth incidence when birth weight dropped below a minimum value, which indicates an optimum birth weight range for calf viability.

Both the involvement of a categorical trait and non-linearity may contribute to the underestimation of the true amount of phenotypic association between dystocia or stillbirth and birth weight. For dystocia score or frequency, correlation estimates on raw data vary between $r = 0.11$ (Foulley et al., 1978; Foulley and Menissier, 1979) and $r = 0.73$ (Couteaudier et al., 1971), commonly centering around $r = 0.3$—0.4 (e.g., Rice and Wiltbank, 1970; Philipsson, 1976c; Burfening et al., 1978a, c). Corresponding estimates for stillbirth occurrence are between $r = 0.06$ and $r = 0.23$ (Philipsson, 1976c; Gaillard, 1980; Meijering and Van Eldik, 1981). To illustrate the effect of correction for discontinuity, some of the coefficients reported were recomputed (Table II). Corrected coefficients indicate that birth weight accounts at maximum for about 50% of phenotypic variance in dystocia and for 20% of variance in stillbirth liability.

TABLE II

Phenotypic correlations between birth weight and dystocia frequency/score or stillbirth incidence before (r_c) and after (r_n) discontinuity correction

Author(s)	Trait	r_c	r_n	Parity
Burfening et al. (1978a)	% Assisted	0.33*	0.36	⩾ 1
Burfening et al. (1978c)	% Assisted	0.29*	0.43	⩾ 1
Gaillard (1980)	% Dystocia	0.41	0.72	1
Gaillard (1980)	% Stillbirth	0.23	0.44	1
Gaillard (1980)	% Dystocia	0.32	0.71	⩾ 2
Gaillard (1980)	% Stillbirth	0.12	0.32	⩾ 2
Hässig and Schlote (1980)	Dystocia score (1—4)	0.33	0.36	1
Meijering and Van Eldik (1981)	% Dystocia	0.32	0.56	2
Meijering and Van Eldik (1981)	% Dystocia	0.40	0.63	2
Meijering and Van Eldik (1981)	% Stillbirth	0.08	0.20	2
Meijering and Van Eldik (1981)	% Stillbirth	0.17	0.35	2

*Residual correlation.

Recording birth weight as an indicator for calf size may be most practical, but it is obvious that, within the FPI concept, calf proportions, as a resultant of skeletal dimensions and muscularity, are crucial. Hässig (1979) examined simple relationships between calving performance score, several height, width and circumference measurements, and a score for muscularity in calves from Fleckvieh heifers. None of these traits showed a higher correlation with calving performance score than birth weight, which is in agreement with the results reported by Couteaudier et al. (1971) and Price and Wiltbank (1978b), girth at the thurls being an exception in Charolais calves from heifers (Couteaudier et al., 1971). When birth weight is kept constant, correlations involving calf dimensions are severely reduced and generally non-significant (Laster, 1974; Hässig, 1979). Multiple correlation coefficients including birth weight, dimensions and muscularity score, as computed by Hässig (1979), were hardly higher than the single correlation with birth weight. This indicates that the part of variance in dystocia rate or score associated with calf dimensions is well accounted for by birth weight alone.

PHENOTYPIC EFFECTS OF SIZE AND SHAPE OF DAM

Within the FPI concept it would be desirable to have measurements indicating the effective size of the genital tract, i.e. the dimensions attainable at the time of expulsion of the calf. As these are hard to obtain, attention has focused on the dimensions of the pelvic inlet before or after parturition, commonly measured as pelvic height (= perpendicular distance from the cranial end of the symphysis pubis to the ventral surface of the midsacrum), pelvic width (largest distance between the shafts of the ilia) and pelvic area (height × width). These internal pelvic dimensions can be measured on the living animal with moderate to reasonable accuracy and repeatability (Ben David, 1960; Menissier and Vissac, 1971; Rice and Wiltbank, 1972; Schlote et al., 1978; Short et al., 1979). It must be stressed however, that they may reflect the size of the pelvic inlet during expulsion inaccurately, as hormonal action during the preparative stage of calving brings about motility in the iliosacral joints, allowing effective pelvic height to be larger than measured (Belic and Menissier, 1968; Schuijt, 1977). Schebitz (1980) observed for instance a 5 cm increase in pelvic height from five days before, up to the day of calving, and a 5—7 cm decrease during the five days afterwards. According to Rüsse et al. (1978), pelvic height may be enlarged by another 15% during abdominal straining. Nevertheless, pelvic inlet dimensions before or after calving seem to be related to dystocia probability up to a certain degree. Young (1968, 1970), Philipsson (1976d) and Steiner (1979) observed a significantly smaller average pelvic inlet in heifers showing dystocia than in those calving without difficulty. Correlations between dystocia score and pelvic height, width or area in heifers of beef breeds were unanimously found to be negative, ranging from $r = -0.10$ to $r = -0.45$ (Rice and Wiltbank, 1970, 1972; Bellows et al., 1971; Couteaudier et al., 1971; Price and Wiltbank, 1978b). These correlations indicate that on average about 10% of the phenotypic variance in dystocia score is associated with variation in pelvic inlet dimensions. If discontinuity of dystocia score is taken into account and if the relationship shows threshold properties, as suggested by Menissier (1975a, b), the true amount of association may be a little higher.

Little information is available on the effect of pelvic inlet area on dystocia probability for a second calf and for older cows. The scarce reports available (Couteaudier et al., 1971; Steiner, 1979) indicate that the effect is similar in direction but probably smaller. One has to consider that other parts of the genital tract may be limiting as well, e.g., the pelvic exit, as suggested by Ben David (1960), or the soft tissues. With respect to the latter, Couteaudier et al. (1971) reported a correlation of $r = -0.44$ between dystocia score and score for intensity of preparation for calving in Charolais heifers.

One may argue that pelvic inlet dimensions are a reflection of general size and/or externally observable properties of the rump, which might be measurable with greater ease and higher accuracy than the internal dimensions and consequently show a stronger relationship with calving ease. In most studies the relationships between body weight or external dimensions and dystocia were, however, essentially zero (e.g., Hansen, 1975a, b; Menissier, 1975b, 1976; Price and Wiltbank, 1978b; Hässig, 1979). Data on the influence of position and external shape of the rump are rare and, at present, rather inconclusive. More research on this point would be desirable.

Occasionally a relationship has been suggested between ease of calving and muscularity or degree of fatness of the dam. Hässig (1979) reported a very low correlation ($r = 0.12$) between dystocia score and score for thigh muscularity in Fleckvieh heifers. Menissier (1976) found no relationship in Charolais heifers, scored for muscularity at 18 months of age and calving at two years of age. Exceptional muscularity (double muscling) may however be accompanied by smaller pelvic inlet dimensions and consequently be detrimental for ease of calving (Hanset and Jandrain, 1979). As to the degree of fatness, Philipsson (1976d) observed a tendency to higher dystocia incidence both in very thin and in obese Friesian heifers, which is in agreement with the weak relationship reported by Bellows et al. (1971) and Laster (1974) for Hereford and Angus heifers.

At this point, it seems justified to conclude that birth weight of calf and pelvic inlet dimensions of dam are the traits with most impact on ease of calving in heifers, as concluded before by Menissier (1975a, b) and Price and Wiltbank (1978a). The determination rate by these traits, as measured by the squared multiple correlation coefficient, is low however, as far as beef breeds are concerned ($R^2 = 0.17$—0.38) (Rice and Wiltbank, 1970, 1972; Laster, 1974; Price and Wiltbank, 1978b; Short et al., 1979). Comparable data for dairy heifers are lacking. Again determination rate will be underestimated due to discontinuity of the dystocia score and probable non-linearity of the relationships. A large part of the variance in the dystocia score is nevertheless not attributable to the two traits mentioned or to other size and shape measurements examined. Part of it might be due to the occurrence of dystocia through other causes than FPI. Moreover, true error variance might be large due to the subjectivity involved in scoring calving performance.

PHENOTYPIC ASSOCIATION WITH GESTATION LENGTH

In reports based on calvings resulting from AI (artificial insemination), gestation length is often analysed in addition to other calving traits, as it is a readily available, accurately assessable trait. Gestation length was repeatedly shown to be phenotypically associated with calving ease, more difficulty occurring, on average, after longer gestation periods (e.g., Banerjee-Schotsman, 1964; Bogner et al., 1970; Philipsson, 1976c). Dreyer (1965) and Philipsson (1976c) pointed out that the relationship shows threshold properties similar to those found in the relationship between birth weight and incidence of calving difficulty. Correlation estimates, ranging from $r = 0.04$ to $r = 0.21$ in both heifers and cows (Pollak, 1975; Menissier, 1976; Philipsson, 1976c; Gaillard, 1980) may therefore underestimate the real amount of association. Philipsson (1976c) also observed a non-linear relationship between gestation length and stillbirth incidence in Friesian heifers, stillbirth frequency being increased after long (> 278 days) as well as short (< 267 days) gestation periods. This phenomenon may add to the very low correlations (r = 0.02—0.06) between stillbirth incidence and gestation time found in Friesian and Fleckvieh heifers and cows (Philipsson, 1976c; Gaillard, 1980; Meijering and Van Eldik, 1981) and it may also account for the lack of difference in average gestation length between live and stillborn calves observed on some occasions (Banerjee-Schotsman, 1964; Cloppenburg, 1966). As birth weight increases by 300—400 g per day in the last month of pregnancy (e.g., Witt et al., 1964; Andersen et al., 1976; Remmen, 1976), it is tempting to assume that the phenotypic relationship between gestation length and dystocia or stillbirth is mediated by birth weight. This idea is made more attractive by the finding of Burfening et al. (1978c) that the association between gestation length and dystocia score or rate of assisted calvings is no longer significant when birth weight is introduced as a covariate.

NON-GENETIC FACTORS

Several factors of non-genetic origin have been examined for their impact on calving performance and stillbirth rate, the most important being dam age or parity, sex of calf, nutritional status of dam and season of calving. Knowledge about their influence may be useful for management. Furthermore adjustments for some of these factors may have to be made in estimating genetic parameters or breeding values. The influence of the factors mentioned will be discussed in association with the phenotypic relationships reviewed in the previous sections.

Age and parity of dam

As it is common practise to let cows calve each year, age and parity are highly confounded. In second calf and older cows, the age of the dam and parity are therefore commonly used synonymously, while age effects have only been studied explicitly in first-calf heifers. There is an overwhelming amount of evidence that both dystocia and stillbirth incidence is much higher at first than at second and later calvings, frequencies reported being three to four times higher for dystocia and two to four times higher for stillbirth in heifers (e.g., Van Dieten, 1963; Pollak, 1975; Gaillard, 1980). Higher stillbirth rates at first calving have also been observed in calvings terminated without difficulty (Van Dieten, 1963; Grommers et al., 1965; Laster and Gregory, 1973). A decreasing tendency in occurrence of dystocia up to the third or fourth parturition has frequently been shown (e.g., Cloppenburg, 1966; Brinks et al., 1973; Burfening et al., 1978a), though differences between second and higher parities may be relatively small (Bar-Anan et al., 1976; Philipsson, 1976b).

Van Dieten (1963) found that age at first calving had no effect on the incidence of dystocia and stillbirth in Dutch Red and White heifers calving between two and three years of age. Non-significant effects were also reported by Cloppenburg (1966) and Berger (1980) for the German Friesian, by

Bar-Anan et al. (1976) for the Israeli Friesian and by Philipsson (1976b) for the Swedish Friesian. Dreyer (1965) observed a slight increase in dystocia incidence with increasing age at first calving in German Friesian heifers between two and three years of age, while Vogt-Rohlf and Lederer (1975) reported a decreasing dystocia incidence for the same breed over the same age range. There is agreement that more calving problems may be expected when heifers calve at a younger (accidents) or a much older age than usual (Lindhé, 1966; Pointer et al., 1975; Philipsson, 1976b). Philipsson's (1976b) conclusion, that the influence of age at first calving will be small when heifers calve in the usual age range and when rearing intensity is adjusted to that age, is therefore very appealing.

Given the much higher dystocia incidence in heifers and the major contribution of FPI to heifer dystocia cases, it is plausible to assume the ratio between calf size and effective pelvic dimensions to be more critical in heifers than in second calf and older cows. Calf size alone cannot be held responsible, as birth weight increases with parity up to the fourth to sixth calving (Dreyer, 1965; Vos et al., 1966; Burfening et al., 1978a). Observations on French beef breed females (Menissier, 1975a) indicate however, that between the ages of two and five, the pelvic inlet area of the dam may increase relatively more than the average birth weight of the calf, which would indeed imply a more favourable ratio between calf size and pelvic inlet dimensions with consecutive parturitions. Higher incidences of dystocia encountered when heifers calve at a relatively young age may be due to a similar cause: poor pelvic development, not fully compensated for by a smaller calf (Philipsson, 1976b). The increased incidence of calving difficulty sometimes observed when dairy heifers calve around three years of age has been attributed to a reduction in elasticity of the pelvis and to accumulation of fat in the pelvic region, which then protrudes into the genital tract (Dreyer, 1965; Cloppenburg, 1966; Philipsson, 1976b). Substantial evidence is, however, lacking. Finally it should be pointed out that the effect of age at first calving has to be considered against the maturity of the breed at a particular age. This is best illustrated by the contrast between the observations in dairy heifers, as discussed above, and those in late-maturing French beef breeds, where dystocia incidence is significantly lower when heifers calve at three years of age than when they calve at two years of age (Menissier et al., 1974, 1981).

Sex of calf

There is general agreement that the sex of the calf is a major source of variance in levels of dystocia and stillbirth, frequencies for male calves being generally about twice as high as for female calves (e.g., Cloppenburg, 1966; Philipsson, 1976b; Hässig and Schlote, 1979). In second-calf and older cows differences between sexes are smaller (Brinks et al., 1973; Burfening et al., 1978a; Gaillard, 1980), and, as far as stillbirth incidence is concerned, occasionally non-significant (Philipsson, 1976b; Remmen, 1976; Lindström and Vilva, 1977). A number of authors (Van Dieten, 1963; Grommers et al., 1965; Laster and Gregory, 1973) have reported non-significant sex differences in stillbirth prevalence when calving was normal, which suggests that the more frequent occurrence of stillbirth in male calves from heifers is mainly due to a higher incidence of dystocia. Sex differences in dystocia frequency may to a large extent be attributable to a difference in size, male calves having larger body dimensions (Wilson, 1973; Philipsson, 1976d) and a 1—3 kg higher average birth weight (e.g., Vos et al., 1966; Burfening et al., 1978a). After correction for difference in birth weight, difference in dystocia rate between sexes is strongly reduced, but has still been found to be significant in a number of studies (e.g., Belic and Menissier, 1968; Philipsson, 1976b; Gregory et al., 1978). Belic and Menissier (1968) suggested that differences in morphology might be responsible, male calves being relatively broader and having a heavier skeleton. There is, however, not much evidence to support this suggestion. Menissier et al. (1974) did not observe significant sex differences in shoulder and thurl width for a given weight, while Philipsson (1976d) found only a significant difference in chest width, but not in hip or thurl width. One should consider that the remaining sex difference might well be due to insufficiency of correction for birth weight, e.g., linear correction for a non-linear relationship.

Levels of nutrition during gestation

The impact of level of nutrition during gestation on calving performance in dairy breeds has not been examined directly. In some papers (Dreyer, 1965; Cloppenburg, 1966; Pijnenburg, 1974) differences in feeding level were supposed to be expressed by herd milk yield and the associations between this trait and dystocia and stillbirth incidence were examined, which is of course a rather rough approach. Data on the amount and the direction of the association between these traits are conflicting, varying from a weak positive correlation, i.e., a higher incidence of calving difficulty in herds with a higher average milk yield (Vogt-Rohlf and Lederer, 1975; Gaillard, 1980), to a weak negative correlation (Lindström and Vilva, 1977), while Dreyer (1965) and Cloppenburg (1966) found no significant association at all. The results lead one to believe that a relationship does not exist.

In beef breeds effects of both low and high levels of nutrition as compared to nutritional standards during the last months of gestation have explicitly been studied, though generally in rather small samples. The results, which were reviewed by Grunert (1979) and Petit (1979), may be transferable to dairy cattle. A severe feed restriction of heifers during the last three months of gestation, resulting in a zero or negative change in body weight, caused a significant reduction in birth weight (e.g., Laster, 1974; Corah et al., 1975; Bellows and Short, 1978). Any influence on calving performance or stillbirth incidence could however either not be shown (Bellows and

Short, 1978; Corah et al., 1975; Young, 1970; Kroker and Cummins, 1979) or was unfavourable (Laster, 1974; Drennan, 1979), probably because pelvic development is also retarded (Young, 1970; Kroker and Cummins, 1979). Vitality of newborn calves may be reduced (Corah et al., 1975; Kroker and Cummins, 1979). Birth weight of calves from older cows seems to be less affected by a similar short-term feed restriction (Drennan, 1979; Petit, 1979), possibly because competition between energy demands for pregnancy and growth is not as pronounced as in heifers (Petit, 1979). Any effects on calving performance have not been shown (Corah et al., 1975; Petit, 1979). If heifers or older cows are fed above standard levels during pregnancy and become obese, this seems to have no effect on birth weight (Arnett et al., 1971; Prior et al., 1979) but calving performance, and consequently stillbirth incidence, may be affected negatively (Arnett et al., 1971; Lowman, 1979) because of fat accumulation in the pelvic region (Grunert, 1979; Lowman, 1979; Petit, 1979). Attempts to prevent calving problems by the application of a feeding regime different from standard shortly before term seem therefore likely to fail.

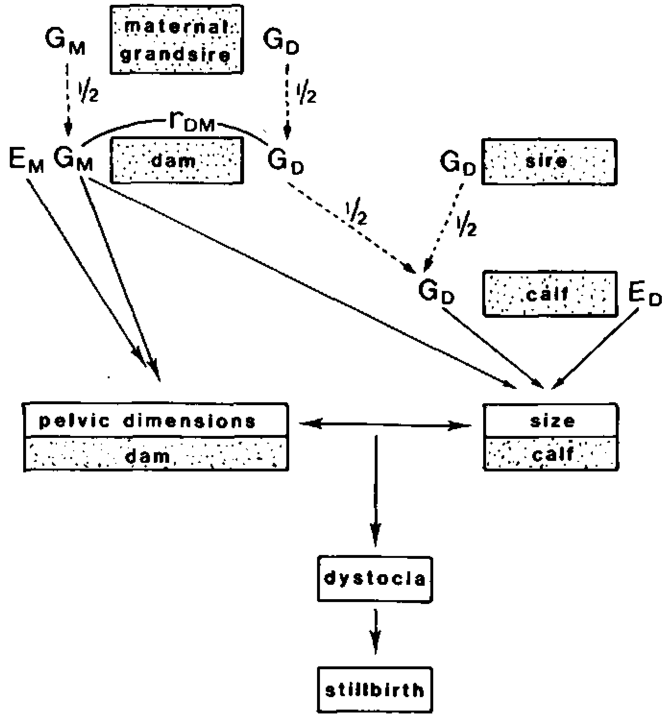
Season of calving

Discussion of the effects of calving season on dystocia and stillbirth incidence will be limited to observations from the North-Western part of Europe, where conditions are familiar to the author. In this region dystocia rate is commonly observed to be a little higher in autumn and early winter (October—December) than in spring and summer, though the seasonal differences may occasionally lack significance (e.g., Van Dieten, 1963; Vogt-Rohlf and Lederer, 1975; Philipsson, 1976b). Data on the seasonal pattern of stillbirth incidence are conflicting. On the one side seasonal variation in stillbirth incidence is reported to be closely associated with fluctuation in dystocia frequency (Van Dieten, 1963; Cloppenburg, 1966; Pijnenburg, 1974), while others have found an increased stillbirth incidence in June and July (Lindhé, 1966; Auran, 1972; Lindström and Vilva, 1977) or have not been able to observe any systematic pattern at all (Vogt-Rohlf and Lederer, 1975; Philipsson, 1975b; Hässig and Schlote, 1979). Higher dystocia frequencies in autumn and winter were found to be associated with a higher average birth weight (Cloppenburg, 1966; Philipsson, 1976b), though Philipsson (1976b) pointed out that seasonal differences in the incidence of dystocia may occur largely independently of birth weight. Other factors which it has been suggested may be involved are day length, associated with hormonal balance (Stegenga, 1964), and amount of exercise (Sejrsen and Neimann-Sørensen, 1979). There is however hardly any evidence to support these suggestions. Philipsson (1976b) and Lindström and Vilva (1977) pointed out that surveillance around parturition is likely to be less intensive during the grazing season, which may be the cause of both a higher stillbirth incidence in summer, as observed by Lindström and Vilva (1977), and of a lower rate of reporting of dystocia cases (Philipsson, 1976b).

Reviewing the non-genetic effects discussed, parity of dam and sex of calf seem to have most impact on dystocia and stillbirth incidence. Adjustment for these factors in genetic analysis is required. Age at first calving may affect calving performance negatively if it is outside the normal range, this range being dependent on breed and management. Levels of nutrition deviating from nutritional standards during the last part of gestation will not improve calving performance in heifers, and may have adverse effects. Feeding level during the rearing period should however be adjusted to age at first calving. In North-Western Europe dystocia incidence tends to show a seasonal pattern, relatively more problems being encountered in autumn and early winter. Data on seasonal patterns in stillbirth occurrence are conflicting. In genetic analysis, the necessity of adjustment for seasonal effects should be examined.

GENETIC EFFECTS

Early studies revealed considerable differences in dystocia and stillbirth incidence between progeny groups of bulls, both as sires (e.g., Van Dieten,



G_D : Genotype for direct inheritance, E_D : Direct environmental effect.
G_M : Genotype for maternal effect, E_M : Maternal environmental effect.
r_{DM} : genetic correlation between direct and maternal genotype.

Fig. 1. Concept of genetic pathways and main target points in dystocia and stillbirth due to feto-pelvic incompatibility (FPI).

1963; Dreyer, 1965; Lindhé, 1966) and as maternal grandsires (Dreyer, 1965; Cloppenburg, 1966; Lindhé, 1966) of newborn calves. Belic and Menissier (1968) were the first to set up a coherent scheme of possible effects on dystocia and stillbirth, encompassing environmental as well as genetic influences of direct and maternal origin. A strongly simplified scheme of genetic action, based on Philipsson (1976c), is shown in Fig. 1. Only FPI-induced dystocia has been considered therein. As to the other major cause of dystocia, malpresentation of the calf, effects of the sire on frequency of malpresentation itself or on dystocia due to malpresentation were found to be essentially zero (Cloppenburg, 1966; Gaillard, 1980; Meijering and Van Eldik, 1981). The influence of the maternal grandsire in this respect has not been studied explicitly. In most genetic studies cases of dystocia due to malpresentation have not been excluded.

Direct genetic effect

Direct genetic effect refers to the influence of calf genotype on calving performance and calf viability. Genetic parameters are generally computed from sire variance and covariance components, from half-sib analysis in field data. ANOVA estimators are derived from linear models applied to raw scores. Estimates of heritabilities and genetic correlations for calving traits, as reported up to 1977, were summarized by Philipsson et al. (1979) and are presented in Table III. More recent estimates by Burfening et al. (1979; 1981), Gaillard (1980), Meijering and Van Eldik (1981) and Thompson et al. (1981) fit well in the ranges given, except for the genetic correlation between stillbirth and birth weight which was found to be higher (r_g = 0.7—0.8) by Gaillard (1980) and Meijering and Van Eldik (1981). Burfening et al. (1978b, c) on the other hand reported higher heritabilities for dystocia (h^2 = 0.21—0.33) and lower genetic correlations between dystocia and birth weight (r_g = 0.24—0.42). With this exception, heritability esti-

TABLE III

Normal ranges of heritability (diagonal; heifers over cows) and genetic correlation (off-diagonal) estimates for dystocia, stillbirth, birth weight and gestation length (Philipsson et al., 1979)

	Dystocia	Stillbirth	Birth weight	Gestation length
Dystocia	0.03—0.20 0.00—0.08	0.6 —0.8	0.9	0.3
Stillbirth		0.00—0.05 0.00—0.02	0.4	0.2—0.3
Birth weight			0.10—0.40 0.10—0.40	0.4—0.5
Gestation length				0.50 0.50

mates for dystocia and especially for stillbirth are relatively low in heifers and even more so in cows. Genetic variability may however be larger than indicated by heritability estimates on a categorical scale (Philipsson et al., 1979), as illustrated by the effect of transformation of h^2 values to the underlying continuous scale (Table IV). Dystocia is genetically very strongly correlated with birth weight ($r_g \simeq 0.9$), leaving hardly any room for selection against dystocia without altering birth weight. Gestation length on the other hand seems to be less closely associated with both dystocia and stillbirth.

TABLE IV

Heritabilities on the categorical scale (h_c^2) and corresponding values on the underlying continuous scale (h_n^2)

Author(s)	Trait	Number of categories	Parity	h_c^2	h_n^2
Tong et al. (1976)	Dystocia	3	Cows	0.10	0.34
Gaillard (1980)	Dystocia	2	Heifers	0.09	0.27
Gaillard (1980)	Dystocia	2	Cows	0.06	0.30
Gaillard (1980)	Stillbirth	2	Heifers	0.04	0.14
Gaillard (1980)	Stillbirth	2	Cows	0.02	0.11
Bar-Anan et al. (1976)	Dystocia	2	Heifers	0.04	0.16
Bar-Anan et al. (1976)	Dystocia	2	Cows	0.01	0.05
Bar-Anan et al. (1976)	Stillbirth*	2	Heifers	0.04	0.13
Bar-Anan et al. (1976)	Stillbirth*	2	Cows	0.01	0.07
Vogt-Rohlf and Lederer (1975)	Dystocia	2	Heifers	0.05	0.26
Vogt-Rohlf and Lederer (1975)	Dystocia	2	Cows	0.01	0.16
Vogt-Rohlf and Lederer (1975)	Stillbirth**	2	Heifers	0.02	0.07
Vogt-Rohlf and Lederer (1975)	Stillbirth**	2	Cows	0.01	0.04

*Including calves dead within 1 week of birth.

**Including calves dead within 48 h of birth.

Utilization of direct inheritance and estimation of direct genetic merit

Though direct genetic variation in dystocia rate would allow successful selection, sire progeny test results are generally only used to recommend bulls for maiden heifers, at least in dairy breeds (Philipsson et al., 1979). By such a strategy, which has already been suggested by Van Dieten (1963), a fast decline of dystocia and stillbirth incidences in the high-risk fraction of the population can be obtained, as demonstrated in theory (Philipsson, 1979), as well as in practise (Bar-Anan et al., 1976; Bar-Anan, 1979). It will however not affect the rate of calving difficulty in the next generation, because the genetic make-up of the population hardly alters (Philipsson et al., 1979). The success rate in such a system in fact depends heavily on the quality of sire evaluation. Problems associated with sire evaluation, like the recording system, adjustments to be made, computation methods and way of expression of genetic merit have been discussed extensively by an EC/EAAP-working group (Philipsson et al., 1979) and recommendations have been made. Three topics in sire evaluation for direct genetic effect will be (re)discussed here, viz. use of all information available, choice of test group and method of estimation.

Without considering pedigree information, the first indications about direct genetic merit of a young bull for ease of calving can be derived from his own gestation period and birth weight. (Rank) correlation estimates were $r \simeq 0.15$ (Pijnenburg, 1974; Meijering and Van Eldik, 1981) and $r = 0.41$ (Remmen, 1976) for the gestation length of a bull and the frequency of stillbirth in his progeny and r = 0.40—0.48 (Remmen, 1976; Meijering and Van Eldik, 1981) for gestation length and dystocia incidence. Figures for birth weight of a bull and stillbirth frequency in his progeny were r = 0.02—0.09 (Lindström and Vilva, 1977). Comparable correlations for birth weight of a bull and dystocia incidence have not been reported. This preliminary information, though being of limited predictive value, may nevertheless be of some value for farmers using a natural service bull for their maiden heifers.

Additional sources of information may be measurements on young bulls and results of performance testing. Significant correlations were reported between body measurements of 25 11-month-old Fleckvieh bulls and the average dystocia score at birth of their progeny (Hässig, 1979; Hässig and Schlote, 1980). Highest estimates (r = 0.4—0.6) were obtained for height at withers, chest width, chest circumference and width at thurls, while the multiple correlation amounted to $r = 0.72$. Similar estimates by Remmen (1976) for measurements on 25 Dutch Red and White bulls and frequency of stillbirth in their progeny were less conclusive. Though correlations for height measurements were significant at two years of age ($r \simeq 0.40$), correlations for all measurements lacked significance ($-0.20 < r < 0.22$) at four years of age. In a study on 353 Fleckvieh bulls in Bavaria, Osterkorn et al. (1979) reported low correlations ($r < 0.16$) between frequencies of stillbirth or veterinarian-assisted calvings on the one hand, and growth rate (over a 420-day test period) and weight/body measurements (at the end of the test period) on the other. Further elucidation of these relationships seems worthwhile, not because a high predictive value is to be expected from these measurements or performance test results, but to assess more accurately the impact of selection on performance test results for future calving performance.

The most valuable information on the direct genetic merit of a young bull is obtained from birth records from his progeny. When heifer mates are used to test young bulls for ease of calving, as recommended by Bar-Anan (1972), Bar-Anan et al. (1976), Burfening et al. (1979) and Philipsson et al. (1979), the benefits of recommending low-risk bulls for heifers are reduced to some degree because relatively high levels of calving problems are expected to be encountered in the fraction required for testing. In order to keep this test fraction as small as possible, while maintaining accuracy of breeding value estimation, different strategies are possible. First, test inseminations may be carried out on cows of all ages, as is usual practise in the U.S.A. (e.g., Thompson et al., 1981) or only on cows in first lactation, as is usual practise in The Netherlands (e.g., Meijering, 1980b). By carrying out most or all of the tests on older cows, detrimental effects of testing are reduced (parity effect), but the efficiency of testing might also be affected. More calvings of older cows have to be recorded in order to obtain the same accuracy as would be achieved by testing on heifers (e.g., Hill, 1977; Philipsson et al., 1979), because of lower heritabilities. In addition, genetic correlations between heifers and cows for direct genetic effect on calving performance may not be unity. Correlations between sire proofs in heifers and cows were reported to be rather low for stillbirth (r = 0.2—0.4; Pijnenburg, 1974; Lindström and Vilva, 1977; Meijering, 1980b), dystocia (r = 0.2—0.6; Burfening et al., 1979; Hudson et al., 1980; Meijering, 1980b) and frequency of caesareans ($r \simeq 0.47$; Hanset and Jandrain, 1979). Genetic correlations, approximated from these estimates by dividing them by the product of accuracies (r_{TI}) of sire proofs in heifers and cows, were r_g = 0.5—0.6 for dystocia and stillbirth in Israeli Friesians (Bar-Anan et al., 1976) and Dutch Friesians (Meijering, 1980b), r_g = 0.75—0.85 for Dutch Red and White cattle (Meijering, 1980b) and $r_g \simeq 1$ for Fleckvieh cattle (Gaillard, 1980). Thompson et al. (1981) obtained a direct estimate of $r_g = 0.84$ for dystocia in Holsteins by multiple trait analysis and concluded that the same genes are involved in heifers and in cows.

If genetic correlations between calving problems in heifers and cows are far from unity, an alternative evaluation strategy, suggested by Bar-Anan et al. (1976) and successfully practised in Israel, might be considered. In this procedure, test bulls are mated with first lactation and/or older cows (but not with heifers) in order to obtain daughters for progeny testing for production traits. A limited number of bulls, selected on the basis of the four-month milk yield of their daughters, are subsequently tested for dystocia incidence when mated with heifers. Using this method, the fraction of heifers required for testing can be limited.

Methods of sire evaluation practised vary from the computation of uncorrected sire frequencies to the use of Best Linear Unbiased Prediction (BLUP). If the records and the genetic merit to be predicted follow a joint normal distribution, BLUP (Henderson, 1973) would be the preferred method, because it gives the maximum likelihood estimator of the best predictor and it maximizes the probability of correct pairwise ranking under these conditions. Schaeffer and Wilton (1976) suggested that the use of BLUP for categorical data might be justified under certain sampling assumptions which, unfortunately, are in conflict with their model. Gianola (1980a, 1982) pointed out that a linear model approach for sire evaluation with categorical data has a number of drawbacks, which would make its use, in theory, less desirable. The most important drawback is probably that best linear predictors may not maximize the probability of correct ranking in this case, because the data are not normally distributed (Portnoy, 1982). Other problems are that sire and error variances are dependent, heteroscedastic and not invariant of the weights assigned to the categories in a polytomous setting (Gianola, 1980a, 1982; Gianola and Norton, 1981). When the linear, equally spaced scoring procedure was compared with more optimal scoring procedures heritability estimates were, however, hardly different (Tong et al., 1977; Gianola and Norton, 1981). In order to avoid scoring problems Quaas and Van Vleck (1980) proposed a multitrait BLUP procedure in which each category of calving performance is considered as a different trait. Apart from conceptual objections that might be raised against this procedure, its use is limited to models with only one random effect.

Non-linear methods of sire evaluation for dichotomous and polytomous traits, based on the logistic distribution, were presented by Gianola. (1980a, b). Gianola and Foulley (1982) proposed an evaluation method for both dichotomous and ordered polytomous traits based on the threshold concept and Bayes' theorem. Though the approach is very appealing from the viewpoint of modelling, the method is, mainly because of an iterative procedure involved, computationally more complicated and more expensive than BLUP. Before implementation, simulation studies should reveal whether the benefits outweigh the additional costs involved.

Sire of dam and maternal effects

As indicated in Fig. 1, the sire of the dam is supposed to act upon calving traits in a more complicated way than the sire of the calf. First, the sire of the dam effect contains a direct genetic component, referring to the contribution of genes to the calf genotype, which is similar to but half of the sire of the calf effect. Furthermore, the sire of the dam may influence calving traits by transmission to his daughters of genes which actually find expression in these daughters as dam of the calf. As to calving traits, this is looked upon as a maternal effect, expressing itself for instance in pelvic dimensions, preparation for calving and/or maternal genetic effect on calf size. Finally an additive genetic correlation between direct and maternal genotype is supposed. Detailed information on the breakdown of genetic effects into direct and maternal components has been presented by Koch (1972) and Willham (1972), while difficulties encountered in estimating appropriate variance components are discussed by Foulley and Lefort (1978) and Willham (1980).

Genetic parameters for total sire of dam effect on calving traits are derived from half-sib daughter group analysis, regarding calving traits as traits of the dam. Heritability and genetic correlation estimates reported up to 1977 were summarized by Philipsson et al. (1979) and are presented in Table V as far as heifer daughter groups are concerned. Estimates from daughter groups of

TABLE V

Normal range of heritability (diagonal) and genetic correlation (off-diagonal) estimates for maternal grandsire effect on dystocia, stillbirth, birth weight and gestation length in heifers (Philipsson et al., 1979)

	Dystocia	Stillbirth	Birth weight	Gestation length
Dystocia	0.03—0.20	0.5 —0.7	0.6 —0.7	0.0
Stillbirth		0.00—0.05	0.3	0.0
Birth weight			0.05—0.20	0.0 —0.4
Gestation length				0.10—0.20

older cows are of less practical value because of their late availability. Moreover, such estimates may be biased because of selection (Philipsson et al., 1979). Recent heritability estimates by Gaillard (1980), Burfening et al. (1981) Thompson et al. (1981) and Benyshek and Little (1982) are within the ranges presented. Estimates for dystocia and stillbirth are of the same magnitude as reported for the direct genetic effect (Table III), and are expected to be biased downwards due to estimation on categorical scales. Estimates obtained after correction for discontinuity (Hansen, 1975a; Lindström and Vilva, 1977) remained, however, within the ranges given. Heritability estimates for maternal grandsire effect on birth weight and gestation length are lower than for direct genetic effect on these traits. Recent estimates for genetic correlations (Gaillard, 1980; Burfening et al., 1981) correspond well with the values given, except for those between gestation length and dystocia and gestation length and birth weight, which Gaillard (1980) found to be higher (r_g = 0.41 resp. r_g = 0.74). Birth weight and gestation length will be of less value in sire evaluation when examining the maternal grandsire effect on dystocia and stillbirth than in evaluation of direct genetic effect, as both heritabilities and genetic correlations are lower (Philipsson et al., 1979).

As outlined by Philipsson (1976c), Gaillard (1980) and Burfening et al. (1981), indirect estimates of direct—maternal covariance and maternal variance can be derived from data including bulls both as sires of calves and sires of dams, though sampling errors may be relatively large. Estimates reported are summarized in Table VI. Direct—maternal genetic correlations tend to be negative for all traits studied, but the estimates vary considerably in size. These figures indicate however, that direct genetic gain for calving problems may be counteracted to some extent by an antagonistic maternal effect. Maternal genetic correlation estimates by Gaillard (1980) suggest that this maternal effect may be at least partially mediated by birth weight ($r_g^M \simeq 0.6$ between birth weight and dystocia or stillbirth). Due to indirect estimation these estimates have to be regarded as approximations (Gaillard, 1980). Maternal heritability tends to be low for all traits considered (Table VI).

TABLE VI

Heritabilities (h^2_M) for maternal effect on calving traits in heifers and genetic correlations between direct and maternal effect (r_{DM})

Author(s)	Dystocia		Stillbirth		Birth weight		Gestation length	
	h^2_M	r_{DM}	h^2_M	r_{DM}	h^2_M	r_{DM}	h^2_M	r_{DM}
Philipsson (1976c)*	0.02	−0.19		0.07	0.02	−0.53	0.05	−0.56
Gaillard (1980)	0.03	−0.63	0.03	−0.68	0.03	−0.11	0.06	−0.51
Burfening et al. (1981)	0.20	−0.53	0.11	−0.24	0.11	−0.24	0.10	−0.38
Thompson et al. (1981)	0.03	−0.38						

*Adjusted heritabilities.

BREEDING CONSIDERATIONS

Reality urges one to acknowledge the secondary importance of dystocia in a breeding program for dairy cattle. Traits under high selection pressure, like milk yield and fat content, were generally found to be essentially uncorrelated with dystocia and stillbirth rates (Lindström and Vilva, 1977; Thompson et al., 1980; Gaillard, 1980), although Bar-Anan (1971) reported favourable correlations. Calving performance in dairy cattle is therefore not expected to deteriorate as a consequence of present selection programs. Selection for beef traits, like body size, growth rate or muscularity, on the other hand will have a detrimental influence on the level of dystocia, as the genetic correlations involved are moderately positive (r_g = 0.2—0.5) (e.g., Foulley et al., 1978; Gaillard, 1980; Thompson et al., 1980), probably through the correlated response in calf size or morphology. In Menissier's (1975b) opinion, calving performance in French beef breeds has deteriorated because of heavy selection for size and muscularity, which simultaneously increased the birth weight and altered the morphology of calves in an unfavourable direction (broader at the shoulders and thurls), while pelvic dimensions did not increase proportionally. Selection indices with restriction on birth weight have been proposed for beef (e.g., Foulley, 1976) as well as for dual purpose cattle (Gaillard, 1980) in order to prevent (further) deterioration of calving performance due to selection for beef traits.

When considering selection against calving problems, there are several possibilities, at least in theory. Model calculations encompassing four alternatives have been presented by Philipsson (1979). First, sire evaluation for direct genetic merit might be used for actual selection, instead of, or in addition to, recommending low risk bulls for heifers. Selection for direct effect would inevitably entail a reduction in birth weight because of the high direct genetic correlation between birth weight and dystocia ($r_g \simeq 0.9$). Birth weight and dystocia are however antagonistic from an economic point of view, as birth weight has shown positive correlations with growth rate and weight at later ages (e.g., Foulley, 1976; Andersen, 1978; Kalm et al., 1978). In some situations, the economic value per unit of birth weight may not justify selection against calving problems (Meijering, 1980a).

Besides the immediate response, selection on direct genetic merit is expected to have a favourable effect on calving performance of the next generation females. In the majority of cases sire merits for direct and maternal grandsire effect were found to be slightly positively correlated for dystocia ($r = 0.53$, Vogt-Rohlf and Lederer, 1975; $r = 0.23$, Pollak and Freeman, 1976; $r = 0.26$, Gaillard, 1980; $r = -0.22$, Burfening et al., 1981), while similar estimates for stillbirth were either slightly negative ($r = -0.15$, Gaillard, 1980; $r = -0.19$, Burfening et al., 1981) or positive ($r = 0.47$, Vogt-Rohlf and Lederer, 1975; $r = 0.52$, Lindström and Vilva, 1977). A guarded conclusion from these correlation estimates may be that future calving problems will at least not increase seriously by considering only genetic merit for direct effect (Pollak and Freeman, 1976). On the other hand, genetic gain by one round of selection is expected to be less than computed from the direct genetic parameters because of a negative direct—maternal covariance (Burfening et al., 1981; Liboriussen, 1981). Furthermore, calving ability of the female progeny in the strict maternal sense would deteriorate (Hanset, 1981), which may be acceptable however, as long as the total response is positive.

Selection on maternal grandsire merit for dystocia, based on evaluation of daughter group results, means selection for an aggregate genotype of antagonistic direct and maternal effects. Theoretical results of such a selection with respect to direct, maternal and total genotype for varying ratios between direct and maternal variance and different direct—maternal genetic correlations have been presented by Hanset (1981). Assuming maternal variance to be one fourth of direct variance and a direct—maternal correlation between —0.5 and 0, selection on maternal grandsire merit yielded a positive response for both the direct and the maternal component, the former being dominant. Total genetic gain was less however, than from selection on direct genetic merit alone. Under the same assumptions, selection for a weighted combination of merits for direct and maternal grandsire effect yielded maximum total gain, but response was predominantly of direct genetic origin. In the long run these alternatives may however be preferable over selection on direct genetic merit only, as maternal calving performance would be maintained or even slightly improved, enabling a reduction in dystocia rate with a less drastic drop in birth weight.

The last alternative to be discussed is selection for the maternal component, or part of it. Separating genetic merit for maternal effect from total maternal grandsire merit will hardly be possible, because of the covariance with the direct genetic component. It might however prove possible to select for single factors that contribute to maternal calving performance but are not involved in this covariance. Although the latter has to be verified, it may be possible to select for pelvic dimensions ($h^2 = 0.2$—0.6; Couteaudier et al., 1971; Benyshek and Little, 1982) or for preparation for calving ($h^2 \simeq 0.14$; Menissier, 1976). Furthermore, Philipsson (1976d) reported that maternal calving performance might be genetically correlated in a favourable sense with low placed thurls and pin bones, i.e., a "roof-shaped" rump. Further verification of these possibilities may be worthwhile.

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RESUME

Meijering, A., 1984. Dystocie et mortalité périnatale chez les bovins: revue des causes, relations et consequences. *Livest. Prod. Sci.*, 11: 143—177 (en anglais).

On passe en revue les recherches sur les difficultés de vêlage (dystocie) et la mortalité périnatale à la fois chez les bovins laitiers et les bovins à viande, qui ont été publiées au cours des deux dernières décennies. On présente brièvement les idées actuelles sur le contrôle hormonal de la parturition. On discute les causes de la dystocie et de la mortalité périnatale et leur contribution aux cas observés sur le terrain, dans la pratique vétérinaire et en clinique obstétrique. On résume les coûts directs (perte de veaux, mort de la mère, travail, frais vétérinaires) et à long terme (taux de réforme, production laitière, fertilité). Après avoir brièvement mentionné les difficultés recontrées dans les estimations de l'héritabilité des corrélations en cas de caractères à expression discrète, et dans leur interprétation, on analyse de façon approfondie les relations phénotypiques entre les performances de vêlage et les caractères du veau, les caractères de la vache et la durée de la gestation. L'influence des facteurs non génétiques (parité, sexe du veau, âge au premier vêlage, saision, plan d'alimentation durant la gestation) et leur mode d'action supposé sont passés en revue. On esquisse le modèle génétique pour les caractéristiques de vêlage et on résume les estimations des composantes supposés être impliqués (facteurs directs et facteurs maternels et interactions entre les deux). Trois aspects de l'évaluation des taureaux quant aux composantes génétiques directes sont discutés de façon approfondie, à savoir: la contribution possible des caractères du taureau (poids à la naissance, durée de gestation, mensurations corporelles, résultats de testage), les possibilités dans le choix des conjoints dans le testage, et les méthodes d'évaluation (BLUP, modèles non linéaires). Enfin, on compare différents stratégies dans la sélections contre la dystocie.

KURZFASSUNG

Meijering, A., 1984. Schwergeburten und Totgeburten bei Rindern: eine Übersicht über Ursachen, Zusammenhänge und Konsequenzen. *Livest. Prod. Sci.*, 11: 143—177 (auf englisch).

Die Forschungsergebnisse der letzten 20 Jahre auf dem Gebiet der Schwer- und Totgeburt bei Milch- und Fleischrindern werden im Hinblick auf Ursachen und Zusammenhänge durchgearbeitet. Das derzeitige Konzept einer hormonellen Kontrolle der Geburt wird kurz skizziert. Die Gründe für Tod- und Schwergeburt werden in Zusammenhang mit den im Felde, in Tierarztpraxen und Kliniken beobachteten Fällen diskutiert. Die direkten (Verlust des Kalbes, Tod der Kuh, Arbeit, Tierarzt) und die Langzeitkosten (Ausmerzrate, Milchleistung, Fruchtbarkeit) werden aufgelistet. Nachdem kurz auf die Schwierigkeiten eingegangen wird die im Falle diskreten Merkmale bei der Schätzung von Heritabilitäten und Korrelationen sowie ihrer Interpretation auftreten, werden phänotypische Zusammenhänge zwischen Abkalbeleistung, Merkmalen des Kalbes und der Kuh sowie Trächtigkeitsdauer ausführlich behandelt. Die Auswirkungen der nicht-genetischen Faktoren (Parität, Geschlecht des Kalbes, Erstkalbelater, Saison, Ernährung während der Trächtigkeit) und ihre vermuteten Wirkungsweisen werden zusammengefasst. Das genetische Modell für die Abkalbemerkmale wird skizziert und die Schätzwerte für die vermutlich beteiligten Komponenten (direkt, maternal, direkt-maternale Interaktion) werden aufgezeigt. Drei Punkte der Evaluierung von Bullen für die direkte genetische Komponente werden angesprochen, nämlich der mögliche Beitrag von Merkmalen des Bullen (Geburtsgewicht, Trächtigkeitsdauer, Körpermasse, Ergebnisse der Eigenleistungsprüfung), die Alternativen bei der Auswahl der Gefährten bei der Nachkommenschaftsprüfung und Evaluierungsmethoden (BLUP, nicht lineare Modelle). Zum Schluss werden alternative Strategien der Selektion gegen die Schwergeburt miteinander verglichen.

Part II

STUDIES ON SIRE EVALUATION FOR CATEGORICAL TRAITS

Chapter 2

Linear versus nonlinear methods of sire evaluation for categorical traits: a simulation study

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Linear versus nonlinear methods of sire evaluation for categorical traits : a simulation study

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Summary

Linear (BLUP) and nonlinear (GFCAT) methods of sire evaluation for categorical data were compared using Monte Carlo techniques. Binary and ordered tetrachotomous responses were generated from an underlying normal distribution via fixed thresholds, so as to model incidences in the population as a whole. Sires were sampled from a normal distribution and family structure consisted of half-sib groups of equal or unequal size ; simulations were done at several levels of heritability (h_y^2). When a one-way model was tenable or when responses were tetrachotomous, the differences between the 2 methods were negligible. However, when responses were binary, the layout was highly unbalanced and a mixed model was appropriate to describe the underlying variate, GFCAT elicited significantly larger responses to truncation selection than BLUP at h_y^2 = .20 or .50 and when the incidence in the population was below 25 p. 100. The largest observed difference in selection efficiency between the 2 methods was 12 p. 100.

Key words : Categorical data, sire evaluation, threshold traits, nonlinear models, simulation.

Résumé

Méthodes linéaires et non linéaires d'évaluation des pères sur des caractères discrets : étude par simulation

Des méthodes linéaires (BLUP) et non linéaires (GFCAT) d'évaluation des pères sur données discrètes ont été comparées à l'aide des techniques de Monte Carlo. On a simulé des réponses selon 2 ou 4 catégories à partir d'une distribution normale sous-jacente munie de seuils fixés. Les pères ont été échantillonnés dans une distribution normale. La structure famille comportait des groupes de demi-germains de taille égale ou inégale. Les simulations ont été effectuées pour plusieurs niveaux d'héritabilité (h_y^2). Les différences entre les 2 méthodes d'évaluation sont négligeables avec un modèle à une voie ou des réponses en 4 classes. Toutefois, en présence de réponses binaires, d'un dispositif fortement déséquilibré et d'une sous-jacente décrite en modèle mixte, la procédure GFCAT procure des réponses après sélection par troncature significativement supérieures à celles obtenues avec le BLUP pour h_y^2 = 0,20 et 0,50 et une incidence du caractère dans la population inférieure à 25 p. 100. La différence maximum d'efficacité de sélection observée entre ces deux méthodes s'est située à 12 p. 100.

Mots clés : Données discrètes, évaluation des pères, caractères à seuils, modèle non linéaire, simulation.

I. Introduction

Prediction of genetic merit of individuals from observations on relatives is of basic importance in animal breeding. If the records and the genetic values to be predicted follow a joint normal distribution, best linear unbiased prediction (BLUP) is the method of choice, because it yields the maximum likelihood estimator of the best predictor, it maximizes the probability of correct pairwise ranking (HENDERSON, 1973) and more relevantly, it maximizes genetic progress among translation invariant rules when selecting a fixed number of candidates (GOFFINET, 1983 ; FERNANDO, 1983). However, a number of traits of importance in animal production (e.g., calving ease, livability, disease susceptibility, type scores) are measured as a response in a small number of mutually exclusive, exhaustive and usually ordered categories. These variates are not normally distributed and, in this case, linear predictors may behave poorly for ranking purposes (PORTNOY, 1982). GIANOLA (1980, 1982) discussed additional potential drawbacks of linear predictors for sire evaluation with categorical data, arguing from the viewpoint of « threshold » models for meristic traits (DEMPSTER & LERNER, 1950 ; FALCONER, 1981).

SCHAEFFER & WILTON (1976) examined a modified version of a (fixed) linear model for analysis of categorical data developed by GRIZZLE *et al.* (1969). They suggested that the use of BLUP methodology in sire evaluation for categorical responses might be justified given certain sampling conditions which unfortunately are inconsistent with the assumptions required by their model. This work gave impetus for widespread use of BLUP in evaluation of sires for categorical variates (e.g., BERGER & FREEMAN, 1978 ; VAN VLECK & KARNER, 1979 ; CADY & BURNSIDE, 1982 ; WESTELL *et al.*, 1982).

GIANOLA & FOULLEY (1983a) developed a Bayesian nonlinear method of sire evaluation for categorical variates based on the « threshold » concept. In this approach (GFCAT = *G*ianola-*F*oulley-*Cat*egorical), the probability of response in a given category is assumed to follow a normal integral with an argument dependent on fixed thresholds and on a location parameter in a conceptual underlying distribution. The location parameter is modeled as a linear combination of fixed effects and random variables. Prior information on the distribution of the parameters of the model is combined with the likelihood of the data to yield a posterior density function, the mode of which is then taken as an approximation to the posterior mean or optimum ranking rule in the sense of COCHRAN (1951), BULMER (1980), FERNANDO (1983) & GOFFINET (1983). Solution of the resulting equations requires an iterative implementation. A conceptually similar method has been developed by HARVILLE & MEE (1982). Although these procedures are theoretically appealing, computations are more complicated than those arising in linear methodology.

Although BLUP has become a standard method of sire evaluation in many countries, its robustness to departures from linearity has not been examined. Non linearity arises with categorical data and, therefore, a comparison between BLUP and the procedure developed by GIANOLA & FOULLEY (1983 a) is of interest. The objective of this paper is to present results of a Monte Carlo comparison of the ability of the above 2 methods to rank sires correctly when applied to simulated categorical data.

II. Methodology

A. *Experimental design and simulation of data*

Three experimental settings were considered to compare the 2 methods of evaluation :

1) a one-way sire model with equal progeny group size within a data set ;
2) a one-way sire model with unequal progeny group size within a data set ; and
3) a mixed model with unequal group size within a data set.

In the 1st setting 36 independent data sets were generated per replicate. These data sets represented all combinations of 3 progeny group sizes (10, 50 or 250 progeny records for each of 50 sires), 3 levels of heritability in a conceptual underlying scale ($h_y^2 = 0.05$, 0.20 or 0.50), and 4 types of categorization which will be described later. Phenotypic values in the underlying scale were generated (RÖNNINGEN, 1974 ; OLAUSSON & RÖNNINGEN, 1975) as :

$$y_{ij} = \frac{1}{2} h_y a_i + a_{ij} \sqrt{\left(1 - \frac{1}{4} h_y^2\right)} \qquad [1]$$

where :

y_{ij} : phenotype of individual j in progeny group i, with $y_{ij} \sim N(0,1)$;
h_y^2 : heritability in the underlying scale ;
a_i : standard normal random variate common to all individuals in progeny group i with $a_i \sim N(0,1)$, and
a_{ij} : standard normal random variate for individual j in progeny group i, with $a_{ij} \sim N(0,1)$.

The phenotypes y_{ij} were categorized using fixed thresholds in the standard normal distribution function. The first 3 categorizations reflected either a 1 p. 100 ($y_{ij} > 2.33$), 5 p. 100 ($y_{ij} > 1.65$) or 25 p. 100 ($y_{ij} > 0.68$) incidence of a binary trait in the population as a whole. The 4th type of categorization created a tetrachotomous trait reflecting incidences of 40 p. 100-40 p. 100-15 p. 100-5 p. 100 in the population as a whole ; this was made using 3 thresholds ($y_{ij} \leq -.25$; $-.25 < y_{ij} \leq .84$; $.84 < y_{ij} \leq 1.65$; $y_{ij} > 1.65$). Binary responses were coded as 0-1, and tetrachotomies were coded using the integer values 1 to 4. The difference in heritability in a categorical scale resulting from using integer verus « optimal » scores is negligible (GIANOLA & NORTON, 1981).

In the 2nd setting 12 independent data sets were generated per replicate, representing all combinations of the above levels of heritability and categorization. However, the 50 progeny groups represented in each data set varied between 5 and 250 in steps of 5. Data were simulated as outlined for Setting 1.

In Setting 3, 15 independent data sets were generated per replicate. Combinations of the 3 heritability levels with a 10 p. 100 incidence level ($y_{ij} > 1.28$) of a binary trait were added to those used in Setting 2. Data were generated as before. Prior to categorization, the effects of 2 fixed classifications, factor A (2 levels) and factor B (10 levels), were superimposed, as indicated in table 1. Each progeny group was almost equally represented in the levels of factor A, but only in 2 levels of factor B (20 p. 100 in level B_ℓ and 80 p. 100 in level $B_{\ell+1}$; $\ell = 1, 3, 5, 7$ or 9). Consequently, 80 p. 100 of the A × B × sire cells had no observations so as to approximate the situation in field data sets. The disconnectedness of data subsets with respect to factor B and sires does not hamper the comparison of predictors of genetic merit, as these are uniquely defined and obtainable regardless of connectedness if the sires are a random sample from one population (FERNANDO *et al.*, 1983). The phenotypic values in the underlying scale modified by the effects of the levels of the A and B factors, were categorized as follows. With $y_{ij} \sim N(0,1)$ as in [1], let :

$$w_{ijk\ell} = y_{ij} + A_k + B_\ell \qquad [2]$$

TABLE 1

Effects of levels of fixed factors A and B, in units of standard deviation, and allocation of progeny to sire groups.

Valeurs des niveaux des effets fixés A et B en unité d'écart-type et répartition des descendances paternelles.

Factor A	Factor B	Progeny group									Total
		1	2	3	4	5	6	7	. . .	50	
1.0	1.0	1	× (a)	×	×	×	3	×	. . .	×	120
	0.8	2	×	×	×	×	12	×	. . .	×	470
	0.6	×	1	×	×	×	×	4	. . .	×	125
	0.4	×	4	×	×	×	×	14	. . .	×	490
	0.2	×	×	2	×	×	×	×	. . .	×	130
	0.0	×	×	6	×	×	×	×	. . .	×	510
	− 0.2	×	×	×	2	×	×	×	. . .	×	135
	− 0.4	×	×	×	8	×	×	×	. . .	×	530
	− 0.6	×	×	×	×	3	×	×	. . .	25	140
	− 0.8	×	×	×	×	10	×	×	. . .	100	550
− 1.0	1.0	0	×	×	×	×	3	×	. . .	×	115
	0.8	2	×	×	×	×	12	×	. . .	×	470
	0.6	×	1	×	×	×	×	3	. . .	×	120
	0.4	×	4	×	×	×	×	14	. . .	×	490
	0.2	×	×	1	×	×	×	×	. . .	×	125
	0.0	×	×	6	×	×	×	×	. . .	×	510
	− 0.2	×	×	×	2	×	×	×	. . .	×	130
	− 0.4	×	×	×	8	×	×	×	. . .	×	530
	− 0.6	×	×	×	×	2	×	×	. . .	25	135
	− 0.8	×	×	×	×	10	×	×	. . .	100	550
		5	10	15	20	25	30	35	. . .	250	6 375

(a) × indicates empty cells.

Clearly, $w_{ijk\ell} \sim N(A_k + B_\ell, 1)$ represents phenotypic values in 20 « sub-populations » corresponding to the filled cells in Table 1. The categories were then formed as :

Incidence and thresholds in N (0,1)	Mapping function	Expected incidence in whole population of table 1
1 p. 100 ; t = 2.33	$w_{ijk\ell} > t$	6.5 p. 100
5 p. 100 ; t = 1.65	$w_{ijk\ell} > t$	15.1 p. 100
10 p. 100 ; t = 1.28	$w_{ijk\ell} > t$	21.6 p. 100
25 p. 100 ; t = .68	$w_{ijk\ell} > t$	34.3 p. 100
40 p. 100 - 40 p. 100 - 15 p. 100 - 5 p. 100 ; t_1 = .25, t_2 = .84, t_3 = 1.65	$w_{ijk\ell} \leq t_1$; $t_1 < w_{ijk\ell} \leq t_2$; $t_2 < w_{ijk\ell} \leq t_3$; $t_3 < w_{ijk\ell}$	43.7 p. 100 - 25.5 p. 100 - 15.7 p. 100 - 15.1 p. 100

In order to limit computing costs, each data set in each setting was replicated 10 times. Further replication depended on the Monte Carlo estimates of the difference between methods of evaluation and of its sampling variance based on the first 10 replicates.

B. *Methods of sire evaluation and computing procedures*

1) In sire evaluations with linear models (BLUP ; HENDERSON, 1973),

$$\mathbf{x} = \mathbf{1}\mu + \mathbf{Zu} + \mathbf{e} \quad \text{(Settings 1 and 2)} \qquad [3]$$

$$\mathbf{x} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Zu} + \mathbf{e} \quad \text{(Setting 3)} \qquad [4]$$

where :

$\mathbf{x}$: vector of categorical responses,
$\mathbf{1}$: vector of ones,
μ : fixed effect common to all observations,
$\mathbf{X}, \mathbf{Z}$: known incidence matrices,
$\boldsymbol{\beta}$: vector of unknown fixed effects,
$\mathbf{u}$: vector of unknown sire effects,
$\mathbf{e}$: vector of residuals.

Assumptions in [3] and [4] were :

$$E(\mathbf{x}) = \mathbf{1}\mu \quad \text{(Settings 1 and 2)} \qquad [5]$$

and :

$$E(\mathbf{x}) = \mathbf{X}\boldsymbol{\beta} \quad \text{(Setting 3)} \qquad [6]$$

Further, in the 3 settings :

$$\text{Var}\begin{bmatrix}\mathbf{x}\\ \mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{ZZ}'\sigma_u^2 + \mathbf{I}_e\sigma_e^2 & \mathbf{Z}\sigma_u^2 & \mathbf{I}_e\sigma_e^2\\ & \mathbf{I}_u\sigma_u^2 & \mathbf{0}\\ \text{symm.} & & \mathbf{I}_e\sigma_e^2\end{bmatrix} \qquad [7]$$

where σ_u^2 and σ_e^2 are the sire and residual variances, respectively, and $\mathbf{I}_u$ and $\mathbf{I}_e$ are identity matrices of appropriate order. With progeny consisting of halb-sib groups :

$$\frac{\sigma_e^2}{\sigma_u^2} = \frac{4 - h_c^2}{h_c^2} \qquad [8]$$

where h_c^2 is « heritability in the categorical scale ». The latter was calculated from the « true » underlying heritability (h_y^2) and from the expected incidences for each of the settings using the formula (VINSON *et al.*, 1976 ; GIANOLA, 1979).

$$h_c^2 = h_y^2 \frac{[\sum_{i=1}^{m-1} z_i (w_{i+1} - w_i)]^2}{[\sum_{i=1}^{m} w_i^2 p_i - (\sum_{i=1}^{m} w_i p_i)^2]} \qquad [9]$$

where *m* is the number of response categories (2 or 4), p_i is the expected incidence in the i^{th} category, $\{z_i\}$ are ordinates of the standard normal density function evaluated at the abscissae corresponding to $\{p_i\}$, and $\{w_i\}$ are the scores assigned to the categories (0-1 or 1-4). Mixed model equations corresponding to the models [3] and [4] were formed using variance ratios as in [8] pertaining to the appropriate levels of heritability used in the simulation. Sire solutions to the mixed model equations were taken as predictors of the transmitting abilities of the 50 sires.

2) In the non linear method (GFCAT ; GIANOLA & FOULLEY, 1983a) the thresholds and the unknown effects which affect location in the conceptual underlying distribution are estimated jointly. The location parameters ($\boldsymbol{\eta}$) were modeled as :

$$\boldsymbol{\eta} = \mathbf{Zu}^* \quad \text{(Settings 1 and 2)} \qquad [10]$$

$$\boldsymbol{\eta} = \mathbf{X}\boldsymbol{\beta}^* + \mathbf{Zu}^* \quad \text{(Setting 3)} \qquad [11]$$

where : $\mathbf{X}, \mathbf{Z}$: known incidence matrices,
$\boldsymbol{\beta}^*$: vector of unknown fixed effects,
$\mathbf{u}^*$: vector of unknown sire effects.

The parameter vector to estimate was either :

$$\boldsymbol{\theta}' = [\mathbf{t}', \mathbf{u}^{*\prime}] \quad \text{(Settings 1 and 2)} \qquad [12]$$

$$\boldsymbol{\theta}' = [\mathbf{t}', \boldsymbol{\beta}^{*\prime}, \mathbf{u}^{*\prime}] \quad \text{(Setting 3)} \qquad [13]$$

In [12] and [13], $\mathbf{t}$ is a vector of unknown fixed thresholds ; t is a scalar when response variables are dichotomous, or a vector of order 3 × 1 when there are 4 categories of response. Prior information about $\mathbf{t}$ and $\boldsymbol{\beta}^*$ was assumed to be vague, and $\mathbf{u}^* \sim \mathbf{N}(\mathbf{0}, \mathbf{I}h_y^2/4)$. The log-posterior density to maximize is :

$$L(\boldsymbol{\theta}) = \sum_{j=1}^{n} \sum_{k=1}^{m} \delta_{jk} \, \ell n \, (P_{jk}) - \frac{1}{2} \mathbf{u}^{*\prime} \mathbf{G}^{-1} \mathbf{u}^* + \text{const.} \qquad [14]$$

where :

n : number of observations,

m : number of categories,

δ_{jk} : Kronecker delta, taking the value 1 if observation j is in category k, and 0 otherwise,

P_{jk} : $\Phi(t_k - \eta_j) - \Phi(t_{k-1} - \eta_j)$, is the probability of response in category k given the location parameter η_j, and $\Phi(.)$ denotes the standard normal distribution function ($t_o = -\infty$, $t_m = \infty$), and

$\mathbf{G}$: Diag $\{h_y^2/4\}$.

The parameters ($\boldsymbol{\theta}$) were estimated iteratively using the modification of the Newton-Raphson algorithm suggested by GIANOLA & FOULLEY (1983a). Starting values used for t were 0 in the case of binary responses, or the threshold values used for categorization into 4 classes when the data were generated. Starting values for $\boldsymbol{\beta}^*$ and $\mathbf{u}^*$ were always zero. In random models, iteration continued until $\boldsymbol{\Delta}' \boldsymbol{\Delta}/p < 10^{-10}$, where $\boldsymbol{\Delta} = \hat{\boldsymbol{\theta}}^{[i]} - \hat{\boldsymbol{\theta}}^{[i-1]}$ is a vector of corrections at the i^th^ iterate, and p is the order of $\boldsymbol{\theta}$. In the mixed model [11] the system does not converge if all responses in a subclass of a fixed effect are in the same extreme category, a problem recognized by HARVILLE & MEE (1982). These authors suggested ignoring the data from such subclasses or to impose upper and lower bounds on the parameter values. In the present study the main interest was in the sire solutions. Because these converge more rapidly than the solutions for $\mathbf{t}$ and $\boldsymbol{\beta}^*$, convergence was monitored by restricting attention to the sire part of the parameter vector. The criterion used was :

$$\{\hat{\mathbf{u}}^{*[i]} - \hat{\mathbf{u}}^{*[i-1]}\}' \{\hat{\mathbf{u}}^{*[i]} - \hat{\mathbf{u}}^{*[i-1]}\}/50 < 10^{-10} \qquad [15]$$

The above test, while suitable for the purpose of this study, cannot be recommended for more general puposes, e.g., field data sets with large numbers of sparsely filled subclasses from combinations of levels of fixed effects.

As the residual standard deviation is the unit of measurement implicit in the method developed by GIANOLA & FOULLEY (1983a), all solutions were multiplied by $\sqrt{1 - h_y^2/4}$ to express them in the scale of the simulation. This, of course, does not affect sire rankings.

C. *Comparison of methods*

The analysis of each data set generated yielded 2 vectors of estimated transmitting abilities (BLUP : $\hat{\mathbf{u}}$; GFCAT : $\hat{\mathbf{u}}^*$) ; the vector of true transmitting abilities ($\mathbf{a}$) was stored during simulation. Sires were ranked using $\hat{\mathbf{u}}$ and $\hat{\mathbf{u}}^*$, and the corresponding average true transmitting abilities for the 10 lowest ranking sires were computed ; let these values be $\bar{a}$ and $\bar{a}^*$ for rankings based on $\hat{\mathbf{u}}$ and $\hat{\mathbf{u}}^*$, respectively. As the categories of response were scored in ascending order, this is tantamount to selection against a « rare » categorical trait or « lower tail selection ». Because of symmetry, only « lower tail selection » needs to be considered. Further, because $E(a_j) = 0$, $\bar{a}$ and $\bar{a}^*$ can be viewed as expressing « effectiveness » of lower tail selection based on $\hat{\mathbf{u}}$ or $\hat{\mathbf{u}}^*$, or as a realized genetic response. The method of evaluation which on average (over replicates) yields the lowest values ($\bar{a}$ or $\bar{a}^*$) would be preferred.

Differences between $\bar{a}$ and $\bar{a}^*$ were examined using paired t-tests within each of the treatment combinations (i.e., progeny group size × heritability × level of categorization). The statistic used is :

$$t_{r-1} = \frac{\bar{d}}{s_{\bar{d}}} \qquad [16]$$

where :

$$\bar{d} = \frac{\sum_{i=1}^{r} (\bar{a}_i^* - \bar{a}_i)}{r} \qquad [17]$$

$$s_{\bar{d}} = \frac{[\hat{V}ar\,(\bar{a}_i^* - \bar{a}_i)]^{1/2}}{\sqrt{r}} \qquad [18]$$

and *r* is the number of Monte-Carlo replicates.

Efficiency of selection, i.e., realized genetic progress as a percentage of maximum genetic progress, was also assessed. Maximum genetic progress was defined as the genetic selection differential occurring if the true transmitting abilities were observable. For example, in the case of selection using BLUP evaluations, efficiency of selection was calculated as :

$$\bar{e} = \frac{100}{r} \sum_{i=1}^{r} \left(\frac{\bar{a}_i}{\bar{a}_i^T} \right) \qquad [19]$$

where $\bar{a}_i^T$ is the average transmitting ability of the sires with the lowest 10 true values.

III. Results

A. *Setting 1*

After 2 replications, it became apparent that the 2 procedures, linear and non linear, gave exactly the same ranking of sires when progeny group size was constant and responses were dichotomous. The log-posterior density in GFCAT (GIANOLA & FOULLEY, 1983a) is equal to :

$$L = \sum_{i=1}^{s} \left\{ (n - n_i)\, \ell n\, [\Phi\,(t - u_i^*)] + n_i\, \ell n\, [1 - \Phi\,(t - u_i^*)] - \frac{2u_i^{*2}}{h_y^2} \right\} + \text{const.} \qquad [20]$$

where :

n : constant progeny group size,
n_i : number or responses for sire i,
t : unknown threshold, and
s : number of sires.

Substituting $v_i = u_i^* - t$ in [20], v_i and t are solved from :

$$\frac{\partial L}{\partial v_i} = \left[\frac{n_i}{\Phi\,(\hat{v}_i)} + \frac{n_i - n}{1 - \Phi\,(\hat{v}_i)} \right] \phi\,(\hat{v}_i) - \frac{4\,(\hat{v}_i + t)}{h_y^2} = 0 \qquad [21a]$$

and

$$\frac{\partial L}{\partial t} = \sum_{i=1}^{s} - \frac{4\,(\hat{v}_i + \hat{t})}{h_y^2} = 0 \quad \Rightarrow \quad \hat{t} = - \frac{1}{s} \sum_i \hat{v}_i = - \bar{v} \qquad [21b]$$

where : ϕ (.) : normal probability density function.

Observe that $\bar{u}^* = \frac{1}{s} \sum_i u_i^* = \bar{v} + t = 0$

It is informative to express n_i in [21a] as a function of v_i, using [21b] :

$$n_i = \frac{4\,(\hat{v}_i - \bar{v})\, \Phi\,(\hat{v}_i)\, [1 - \Phi\,(\hat{v}_i)]}{h_y^2\, \phi\,(\hat{v}_i)} + n\, \Phi\,(\hat{v}_i) \qquad [22]$$

It can be shown (proof available on request) than n_i is a monotonically increasing function of $\hat{v}_i$, and hence of $\hat{u}_i^*$. It is easy to see that this is the case by replacing $\Phi(v_i)$ by its logistic approximation (GIANOLA & FOULLEY, 1983a) so :

$$n_i = \frac{4(\hat{v}_i - \hat{w})}{h_y^2} + n\,[1 + e - \hat{v}_i]^{-1} \qquad [23]$$

which is clearly a monotonically increasing function of $\hat{v}_i$ and thus of $\hat{u}_i^*$. Because of the monotonicity, as n_i increases, so does $\hat{u}_i^*$. Similarly, in BLUP, when $\mu = 0$, the transmitting ability of the sire is calculated from :

$$\left[n + \frac{4 - h_c^2}{h_c^2}\right]\hat{u}_i = n_i \qquad [24]$$

so $\hat{u}_i$ is a linear and, therefore, monotonically increasing function of n_i. We conclude that for a one-way random model, binary responses and constant progeny group size :

$$n_i > n_j \quad \Rightarrow \quad \hat{u}_i^* > \hat{u}_j^* \quad \Rightarrow \quad \hat{u}_i > \hat{u}_j$$

so GFCAT and BLUP yield exactly the same ranking of sires.

With 4 categories of response and constant progeny group size, BLUP and GFCAT gave, in general, similar sire rankings (table 2). The average difference (eq. [17]) between methods was generally not significant and lower than 2 p. 100, except for

TABLE 2

Effects of lower tail selection (10 sires out of 50) using BLUP and GFCAT[(a)] *: one way random model, constant progeny group size and tetrachotomous responses (Average of 10 replicates).*

Effets d'une sélection sur la partie inférieure de la distribution (10 pères retenus parmi 50) en utilisant le BLUP ou GFCAT : modèle aléatoire à 1 facteur, nombre constant de descendants, réponse en 4 catégories (moyenne de 10 réplications).

h_y^2	n [(d)]	h_c^2	Mean true T.A. of sires selected by :		SD [(b)]	Significance [(c)]	Efficiency (%)	
			BLUP	GFCAT			BLUP	GFCAT
0.05	10	0.041	− 0.324	− 0.310	0.162	NS	22.9	21.9
	50		− 0.892	− 0.910	0.072	NS	61.6	63.2
	250		− 1.207	− 1.217	0.040	NS	82.1	82.9
0.20	10	0.163	− 0.826	− 0.832	0.085	NS	61.4	61.7
	50		− 1.167	− 1.181	0.043	NS	80.0	81.0
	250		− 1.363	− 1.366	0.009	NS	95.6	95.8
0.50	10	0.407	− 1.038	− 0.977	0.066	*	76.8	72.4
	50		− 1.393	− 1.392	0.021	NS	92.8	92.7
	250		− 1.283	− 1.283	0.015	NS	97.9	97.9

(a) Symbols defined in text.
(b) Standard deviation of difference.
(c) NS : not significant ; * : $P < .05$.
(d) Progeny group size.

$h_y^2 = .50$ and n = 10. In this case, BLUP was « better » in 7 of the 10 replicates, and equal to GFCAT in the remaining 3 ; for this combination of h_y^2 and n BLUP was 4.4 p. 100 better than GFCAT, ($p < .05$). However, in view of the overall pattern of results in Table 2, it is doubtful whether this « significance » should be taken seriously. As expected, the efficiency of selection as defined in this paper increased with h_y^2 and, particularly, with n. The results indicate a « consistency » property of the 2 methods : as n increases, BLUP and GFCAT converge in probability to the true transmitting ability of a sire, and more rapidly so at a higher level of heritability.

B. *Setting 2*

When the data were described by a one-way random model and progeny group size was variable (5 to 250 progeny per sire), BLUP and GFCAT did not always yield the same sire rankings (Table 3). However, on the basis of 10 replications, the 2 methods gave virtually similar results, as indicated by the almost null variance of their difference. As in the previous case, the efficiency of selection increased with heritability and incidence, and also with the extent of polychotomization (binary vs. tetrachotomous variables).

TABLE 3

Effects of lower tail selection (10 sires out of 50) using BLUP and GFCAT (a) : one way random model with unequal progeny group sizes (Average of 10 replications).

Effets d'une sélection sur la partie inférieure de la distribution (10 pères retenus sur 50) en utilisant le BLUP ou GFCAT : modèle aléatoire à 1 facteur avec un nombre variable de descendants par père (moyenne de 10 réplications).

h_y^2	Incidence (%)	h_c^2	Mean true T.A. of sires selected by :		SD (b)	Efficiency (%)	
			BLUP	GFCAT		BLUP	GFCAT
0.05	1	0.004	− 0.397	− 0.397	0	27.5	27.5
	5	0.011	− 0.591	− 0.579	0.036	40.7	39.8
	25	0.027	− 0.990	− 0.990	0	70.3	70.3
	IV (c)	0.041	− 1.112	− 1.111	0.075	74.0	74.0
0.20	1	0.014	− 0.670	− 0.674	0.036	49.6	49.8
	5	0.045	− 0.941	− 0.941	0	71.4	71.4
	25	0.108	− 1.115	− 1.115	0	85.9	85.9
	IV (c)	0.163	− 1.234	− 1.236	0.005	86.9	87.1
0.50	1	0.035	− 0.879	− 0.879	0	60.8	60.8
	5	0.112	− 1.143	− 1.124	0.044	81.3	79.9
	25	0.269	− 1.257	− 1.261	0.013	89.4	89.7
	IV (c)	0.407	− 1.381	− 1.390	0.031	95.3	95.8

(a) Symbols defined in text.
(b) Standard deviation of difference.
(c) Tetrachotomous response (40 p. 100 - 40 p. 100 - 15 p. 100 - 5 p. 100).

C. *Setting 3*

Under the more realistic assumptions of this setting, GFCAT performed significantly better than BLUP when responses were binary, heritability in the underlying scale was moderate ($h_y^2 = .20$) or high ($h_y^2 = .50$), and when low incidences (1 p. 100, 5 p. 100) were used to categorize the underlying variate (Table 4). GFCAT was also better when $h_y^2 = .50$ and incidence was 10 p. 100. In these instances, the increase in efficiency ranged between 3.9 p. 100 ($h_y^2 = .50$ and 5 p. 100 incidence) to 12.2 p. 100 ($h_y^2 = .20$ and 1 p. 100 incidence). The 2 methods did not differ significantly at $h_y^2 = .05$, or when the incidence of a binary trait was 25 p. 100, or when the response was tetrachotomous.

TABLE 4

Effects of lower tail selection (10 sires out of 50) using BLUP and GFCAT (a) *: mixed model with unequal progeny group sizes (Average of 20 replicates).*

Effets d'une sélection sur la partie inférieure de la distribution (10 pères retenus parmi 50) en utilisant le BLUP ou GFCAT : modèle mixte avec un nombre variable de descendants par père (moyenne de 20 réplications).

h_y^2	Incidence (%)	h_c^2	Mean true T.A. of sires selected by :		SD (b)	Significance (c)	Efficiency (%)	
			BLUP	GFCAT			BLUP	GFCAT
0.05	1	0.013	− 0.594	− 0.611	0.159	NS	42.7	44.3
	5	0.021	− 0.675	− 0.682	0.093	NS	47.1	47.6
	10	0.026	− 0.757	− 0.732	0.108	NS	53.4	51.6
	25	0.034	− 0.875	− 0.860	0.081	NS	59.4	58.3
	IV (d)	0.040	− 0.791	− 0.782	0.093	NS	60.1	59.3
0.20	1	0.053	− 0.646	− 0.771	0.237	*	47.0	55.8
	5	0.085	− 0.868	− 0.942	0.134	*	63.6	69.0
	10	0.102	− 0.955	− 0.978	0.094	NS	69.9	71.5
	25	0.136	− 1.108	− 1.116	0.093	NS	77.0	77.5
	IV	0.161	− 1.080	− 1.081	0.083	NS	77.5	77.5
0.50	1	0.134	− 0.775	− 0.950	0.210	**	55.6	67.8
	5	0.215	− 1.007	− 1.063	0.110	*	73.5	77.4
	10	0.255	− 1.080	− 1.203	0.208	*	74.4	82.3
	25	0.339	− 1.129	− 1.124	0.066	NS	86.3	86.2
	IV	0.402	− 1.264	− 1.276	0.072	NS	89.2	89.7

(a) Symbols defined in text.
(b) *Standard deviation of difference.*
(c) * $p < .05$; ** $p < .01$; NS : not significant.
(d) *Tetrachotomous response (see text).*

As pointed out before, the intended incidence levels in the mixed model setting do not correspond to the realized incidence levels ; the reason for this is that each combination of fixed effects represents a distinct statistical population.

IV. Discussion

This study addressed ranking properties of linear (BLUP) and non-linear (GFCAT) methods of sire evaluation for dichotomous or ordered categorical responses. The end-point measured was the Monte Carlo realized response to truncation selection upon predicted sire values. The impetus for the study was provided by shortcomings expected in theory when linear predictors are used with categorical responses (GIANOLA, 1980, 1982) ; these shortcomings are addressed by GFCAT. As BLUP has become in many countries the standard procedure for sire evaluation, a change in methodology for certain traits could be justified only if the alternative method, in this case GFCAT, leads to improved selection decisions. This was the rationale for the choice of end-point measured.

Under normality, BLUP is the maximum likelihood estimator of E ($\mathbf{u} \mid \mathbf{y}$) or best predictor (HENDERSON, 1973). The best predictor maximizes the correlation between true and predicted values, or accuracy of selection (HENDERSON, 1973 ; BULMER, 1980). In order to illustrate, consider a one-way sire model with known mean. If the sires are unrelated, the squared accuracy of selection for the i^th^ sire, using the best linear predictor as a ranking rule, is :

$$\rho_i^2 = n_i \Big/ \left[n_i + \frac{4 - h_c^2}{h_c^2} \right] \qquad [25]$$

However, under the threshold model and with binary responses (DEMPSTER & LERNER, 1950) :

$$h_c^2 = \frac{\phi^2(t)}{\Phi(t)\,[1 - \Phi(t)]}\, h_y^2 = w\, h_y^2 \qquad [26]$$

where $t = \Phi^{-1}(\alpha)$ is the inverse probability transformation corresponding to an overall incidence α in the population. Using [26] in [25], it is clear that ρ_i^2 increases with w at a given h_y^2. However w is maximum when $t = 0$ (α = 50 p. 100), and symmetric about this value. Hence, ρ_i^2 is frequency dependent, and the accuracy of selection of a linear predictor declines as α departs from 50 p. 100, irrespective of the direction. Although ρ_i is only an approximate measure of efficiency of selection when E ($\mathbf{u} \mid \mathbf{y}$) is not linear in $\mathbf{y}$ (BULMER, 1980), the above argument illustrates the impact of the incidence of a binary trait on efficiency of selection (see, for example, table 3). In GFCAT, the posterior density is well approximated by a multivariate normal distribution as the margins of the contingency table (GIANOLA & FOULLEY, 1983a) become large. In a one way-sire model, the squared accuracy of selection with GFCAT is approximately :

$$\rho_i^{*2} = n_i w_i^* \Big/ \left[n_i w_i^* + \frac{4 - h_y^2}{h_y^2} \right] \qquad [27]$$

where :

$$w_i^* = \frac{\phi^2(t - u_i)}{\Phi(t - u_i)\,[1 - \Phi(t - u_i)]} \qquad [28]$$

and u_i is the transmitting ability of the i^th^ sire in the underlying scale. Note that the accuracy of selection depends not only on n_i and h_y^2 but on the distance between the true transmitting ability of the i^th^ sire and the threshold. This is automatically estimated in GFCAT and not taken into account in BLUP. Nevertheless, [27] is maximum when $t = u_i$, and decreases as the proportion of the progeny of the sire exhibiting a response deviates from 50 p. 100. This is also borne out by the results in table 3. All in all, the results in tables 2 and 3 clearly suggest that BLUP, as measured by the criterion considered in this study, is a very satisfactory method of prediction of breeding value for categorical responses when the one-way sire evaluation model is tenable. In view of the lower computational requirements of BLUP relative to GFCAT, the adoption of non linear methodology is difficult to justify in this type of sampling scheme.

In one-way layouts, many assumptions violated by linear models when applied to binary responses are not strained (GIANOLA, 1980, 1982). For example, the phenotypic variance, $\Phi(t)\,[1 - \Phi(t)]$, is homogeneous. This is not true in the mixed model situation where, in the usual notation (e.g., GIANOLA & FOULLEY, 1983b), the residual variance is $\Phi(\mathbf{X}\boldsymbol{\beta} + \mathbf{Zu})\,[1 - \Phi(\mathbf{X}\boldsymbol{\beta} + \mathbf{Zu})]$. When a mixed model was applied to generate and to analyze the data, GFCAT was significantly better than BLUP in a number of heritability-incidence combinations for binary responses (table 4). This occurred at $h^2_y = .20$ and $.50$, and when incidence was low. Note that at these levels of h^2_y, the heritability in the « observed » scale for the significant comparisons varied between .05 and .26, depending on the incidence. The range of incidences encompassed by the significant comparisons was 1 p. 100 (6.5 p. 100 of « effective incidence » ; see previous sections) to 10 p. 100 (21.6 p. 100 of « effective incidence »). It is not immediately obvious, at least when responses were binary, why « significance » occurred for some treatment combinations but not for others. Because a plot of the standard normal distribution function against its argument is particularly non linear in the tails, we conjecture that a linear approximation is fairly robust at intermediate frequencies, say 20 to 80 p. 100, but breaks down otherwise. The levels of incidence (1-10 p. 100, or effectively 6.1 p. 100-21 p. 100) and the « observed » heritabilities (.05-.26) at which « significances » occurred, suggest that GFCAT should be considered for application to genetic evaluation of binary traits related to reproduction and fitness, e.g., calf survival, conception rate, or abortion rate under tropical or sub-tropical conditions (A. MENENDEZ, Cuba ; personal communication). When responses were tetrachotomous the 2 methods did not differ significantly for any of the treatment combinations considered. This suggests that the linear combination $\mathbf{w}'\mathbf{v}$ ($\mathbf{w}$: vector of scores ; $\mathbf{v}$: 4×1 vector containing the observations in the 4 categories for a particular subclass) tends to normality rapidly so that a linear approximation does not result in any appreciable loss in response to selection.

A conceptual difficulty encountered when implementing the linear analysis in the simulation under the assumptions of a mixed model, was arriving at a meaningful value of h^2_c. In a single population problem, h^2_c can be readily calculated from h^2_y and from the incidences in the population (ROBERTSON, 1950 ; VINSON *et al.*, 1976 ; GIANOLA, 1979) ; simulation studies conducted by VAN VLECK (1972) and OLAUSSON & RÖNNINGEN (1975) suggest that this approximation is fairly accurate, at least for binary responses. However, under a mixed model, there are as many h^2_c's as there are combinations of levels of fixed effects or sub-populations (GIANOLA, 1980, 1982). This implies that the variance ratio used in BLUP would need to vary from sub-population to sub-population. However, because a sire leaves progeny in many sub-populations, this poses the problem of which variance ratio applies to which sire. The approach taken in this paper, e.g., for binary responses, was to approximate h^2_c as :

$$h^2_c = \frac{h^2_y\,\bar{\phi}^2}{\bar{\Phi}\,(1 - \bar{\Phi})} \qquad [29]$$

where :

$\bar{\Phi}$: $\sum_i p_i\Phi_i$, with Φ_i being the incidence in the sub-population i ;

p_i : proportion of observations in the data set in the i^{th} sub-population ;
$\bar{\phi}$: ordinate of the standard normal density function appropriate to $\bar{\Phi}$.

TABLE 5

Efficiency (p. 100) of lower tail selection (10 sires out of 50) using BLUP, as a function of « operational » heritability : mixed model setting and dichotomous responses (Average of 10 replications).

Efficacité (en p. 100) d'une sélection par le BLUP sur la partie inférieure de la distribution (10 pères retenus parmi 50) en fonction de la valeur opérationnelle de l'héritabilité : modèle mixte et réponses tout-ou-rien (moyenne de 10 réplications).

Incidence	« Operational » heritability	Underlying heritability		
		.05	.20	.50
1 p. 100	$\left(\frac{1}{2}\right) h_c^2$	40.6	58.8	54.4
	$\left(\frac{3}{4}\right) h_c^2$	40.8	57.2	53.2
	h_c^2	40.9	56.3	52.9
	$\left(\frac{5}{4}\right) h_c^2$	41.4	55.2	51.6
	$\left(\frac{3}{2}\right) h_c^2$	40.2	54.0	50.8
5 p. 100	$\left(\frac{1}{2}\right) h_c^2$	37.2	70.0	75.7
	$\left(\frac{3}{4}\right) h_c^2$	38.0	71.7	77.1
	h_c^2	39.5	70.3	77.1
	$\left(\frac{5}{4}\right) h_c^2$	39.3	68.9	77.1
	$\left(\frac{3}{2}\right) h_c^2$	39.2	69.3	77.2

While this is a heuristic solution, to which alternatives exist, the difficulty of modeling correctly the threshold concept with linear models is well illustrated. It is possible to speculate that use of an « incorrect » heritability might have affected negatively the effectiveness of selection using BLUP as a sire ranking criterion. Mixed linear model predictors of breeding value are believed to be insensitive to changes in heritability (FREEMAN, 1979). We examined this problem for the case of binary responses via an additional simulation. Six data sets were generated under the mixed model assumptions of Setting 3 ; the data sets corresponded to 2 levels of incidence in the population (1 p. 100 or 5 p. 100), and 3 levels of heritability (h_y^2 = .05, .20 or .50). In each data set, the value of h_c^2 used in the mixed model computations was varied from 50 p. 100 to 150 p. 100 of the « true » h_c^2. As shown in table 5, the efficiency of selection averaged over 10 replications was virtually insensitive to the value of h_c^2 used in the calculations.

GFCAT is based on the concept of an underlying continuous distribution of genetic merits and environmental influences. The data simulation procedure applied implicitly assumes this concept to be reality. In many cases the evidence to support this concept may not be sufficient however. A trait may be categorical down to the genetic level (e.g. halothane sensitivity in pigs). On theoretical grounds both methods compared would be hard to justify then.

V. Conclusions

The results of this study indicate that a non linear method of sire evaluation for categorical responses, GFCAT, does not always outperform BLUP. In the one-way sire evaluation models, differences between methods, as measured by the ability to elicit larger response to selection, were negligible. However, this type of layout is seldom realistic in practice. Similarly, when responses were polychotomous, i.e., more than 2 meaningful categories of response, there was little difference between methods, irrespective of the model used to generate and to analyze the data. In the above cases, given the additional computational requirements of GFCAT and the apparent robustness of BLUP, it seems doubtful that non linear methodology could be justified from a practical point of view.

When a mixed model was required to describe variation of binary responses, GFCAT performed significantly better than BLUP when heritability in the conceptual underlying scale was moderate to high, and when the expected incidence was below 25 p. 100 ; for some combination of parameters the gain in efficiency of selection amounted to 12 p. 100. Hence, it appears that for the type of sampling situations that arise in animal breeding practice, non linear methods should be given serious consideration for the analysis of binary responses. At least in theory, it is expected that the superiority of GFCAT over BLUP would be proportional to the number of fixed effects required in the model and to the extent of heterogeneity in incidence across statistical sub-populations.

The cost of data processing is usually small relative to the other outlays associated with a large scale breeding program, e.g., field personnel, testing facilities, and overhead costs. Small increases in accuracy of selection stemming from improved evaluations of candidates are usually cost effective because the total cost of the evaluation is increased only to a limited extent. Further, the improved evaluations have multiplicative effects as potentially increased returns from improved stock are spread industry-wide (albeit unequally among tiers) and over generations. In the data sets considered in the present study between 5 to 10 rounds of iteration were required to attain convergence using GFCAT. This may give an indication of the additional computational requirements of the non linear methodology.

In the present study, the underlying variance-covariance structure was known. This might have favored GFCAT somewhat over BLUP because the prior distribution for the former method could be specified without « error ». As pointed out previously, when applying linear methodology to categorical responses a « heritability » value needs to be contrived ; in the general case it is not obvious how to do this. However, the results displayed in table 5 suggest that this issue should not have been an important source of difference between the 2 methods. On the other hand, it is possible that the linear methodology was « helped » by using a contrived value of heritability. This is so because of the inability of linear methods to account for the relationship between mean and variance arising in categorical responses. Methods for estimating variance components in mixed linear models (at least 10 such methods have been described in the literature !) may give severely biased estimates of the underlying variance-covariance structure. This is an area for further work. Clearly, a single simulation study cannot address all possible combinations of parameters, data structures, models and methods.

A question of considerable interest is the ability of BLUP versus GFCAT to account for selection bias. While under normality BLUP is unbiased by selections based on translation invariant functions of the records (HENDERSON, 1973 ; FERNANDO, 1983 ; GOFFINET, 1983), this property does not hold for other distributions, e.g. multinomial. FERNANDO (1983) has shown that when selecting a fixed number of candidates, genetic progress is maximized by ranking individuals with conditional means, calculated as if selection had not occurred, irrespective of the number of stages or of generations involved in the selection program. With categorical responses, GFCAT can be thought of as an approximation to the posterior mean or conditional expectation of the predictands given the data. We conjecture that GFCAT should be less prone to bias than BLUP for categorical data in a population undergoing selection.

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Chapter 3

Observations on sire evaluation with categorical data using heteroscedastic mixed linear models

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Observations on Sire Evaluation with Categorical Data Using Heteroscedastic Mixed Linear Models

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ABSTRACT

The ability of three mixed linear models to rank sires correctly for dichotomous and ordered tetrachotomous traits was studied using simulated half-sib progeny data. The models differed in the assumptions made regarding homogeneity of residual variance. Ranking ability was assessed by estimating the realized response to truncation selection (20% of the candidates selected) upon sire evaluations in populations consisting of 50 such sires. Results suggested that weighting for unequal residual variances, in spite of reducing apparent prediction error variance, impairs the ability of best linear unbiased prediction to identify superior sires. This is consistent with theoretical arguments stemming from threshold models.

INTRODUCTION

When the records and the transmitting abilities of sires follow a joint normal distribution, the best linear unbiased predictor (BLUP) is the maximum likelihood estimator of the best predictor and it maximizes the probability of correct pairwise ranking of candidates for selection (11). Further, under normality, BLUP maximizes genetic progress among location invariant selection criteria when selecting a fixed number of candidates (4, 9). With categorical responses, normality is not a tenable assumption, and linear predictors may be poor for ranking purposes (16).

A common approach in genetic analysis of ordered categorical variates is to postulate a hypothetical underlying normal distribution of "liability" comprising genetic and environmental components (2, 3). The position of a realized value of this conceptual variable with respect to a set of fixed thresholds determines the observed category of response. Methods of sire evaluation based on the threshold concept have been developed recently (7, 10). Genetic merits are estimated in the underlying scale by modeling the argument of a normal integral as a linear combination of thresholds, fixed effects, and random variates (7). The methods yield nonlinear equations requiring iterative solution, so they are computationally more involved than linear prediction in the observable (categorical) scale. Meijering and Gianola (14), using simulation, reported that a nonlinear predictor (7) improved sire rankings over those obtained with BLUP in the observable scale. This occurred under highly unbalanced mixed model layouts when the responses were binary, the heritability of liability was between 20 and 50%, and the expected incidence of the trait was lower than 25%. With ordered tetrachotomous traits, the methods gave virtually the same rankings.

Under the threshold model, the expectation and dispersion structures depend on the frequencies and on the weights assigned to different categories (8). Berger and Freeman (1) studied prediction of sire merit for dystocia using BLUP. They compared a homoscedastic model with one in which the residual variance changed with parity of dam (of calf). Because the second model reduced prediction error variance (PEV) substantially, the authors concluded that the weighting procedure was a significant improvement over the homoscedastic model. However, if one argues from the threshold model, BLUP is not an unbiased procedure (8). Hence, comparison in terms of mean squared error of prediction (12, 13), the sum of PEV and squared prediction bias would be more sensible. Unfortunately, an examination

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of the bias is not feasible with field data, as the true genetic merits are unknown.

The objective of this study was to compare mixed linear models with different residual error variances in terms of their ability to elicit genetic change for binary and ordered polychotomous variates. Computer simulation was used for this purpose.

MATERIALS AND METHODS

Design and Simulation of Data

Twelve independent data sets were generated in each of 20 Monte Carlo replications of the experiment. The data sets corresponded to all combinations of three levels of heritability in the underlying scale (h_y^2 = .05, .20, .50) and four types of categorization, which will be described later. The records in each data set were simulated (15, 17) using the model:

$$w_{ijkl} = A_i + B_j + y_{kl} \qquad [1]$$

where A_i and B_j are fixed and $y_{kl} \sim N(0,1)$. Further:

$$y_{kl} = .5\, h_y b_k + c_{kl}\sqrt{1-.5h_y^2} \qquad [2]$$

where:

b_k = N(0,1) variate common to individuals in sire progeny group k (k=1, . . ., 50), and

c_{kl} = N(0,1) variate peculiar to individual l in progeny group k, and independent of b_k. Progeny group sizes varied, in steps of 5, from 5 to 250.

Factors A and B in [1] had 2 and 10 levels as shown in Table 1. Each progeny group was almost equally represented in both levels of factor A but only in two levels of factor B (20% in B_j and 80% in B_{j+1}; j=1,3,5,7,9). Thus, 80% of the AB cells were empty, a situation frequently encountered in field data sets. Although the layout yields five disconnected data sets with respect to factor B and sires, this is immaterial regarding evaluation of transmitting ability via BLUP to the extent that the definition of the latter does not include levels of B (5).

The four types of categorization and the scores for each of the categories were as follows:

1) Binary responses = 0 if $w_{ijkl} < 2.33$ and 1 otherwise. Although a threshold value of 2.33 gives an incidence of 1% in N(0,1), this yielded an expected incidence of 6.5% in the layout of Table 1.
2) Binary responses = 0 if $w_{ijkl} < 1.65$ and 1 otherwise. Expected incidence in layout of Table 1 is 15.1%.
3) Binary responses = 0 if $w_{ijkl} < .68$ and 1 otherwise. Expected incidence is 34.3%.
4) Tetrachotomous responses = 1 if $w_{ijkl} \leq -.25$; 2 if $-.25 < w_{ijkl} \leq .84$; 3 if $.84 < w_{ijkl} \leq 1.65$; and 4 if $w_{ijkl} > 1.65$.

The expected incidences in the population defined by Table 1 are 43.7, 25.5, 15.7, and 15.1% for categories 1 through 4, respectively.

Models

The records were modeled for analysis as:

$$\mathbf{Y} = \mathbf{X}\underset{\sim}{\beta} + \mathbf{Zu} + \mathbf{e} \qquad [3]$$

where **Y** is an n × 1 vector of categorical responses, $\underset{\sim}{\beta}$ is a 12 × 1 vector of fixed effects associated with factors A and B, **X** and **Z** are known instance matrices, **u** is a 50 × 1 vector of transmitting abilities (random), and **e** is a vector of residuals. Additional assumptions were:

$$E(\mathbf{Y}) = \mathbf{X}\underset{\sim}{\beta} \qquad [4]$$

$$E(\mathbf{u}) = 0 \qquad [5]$$

$$E(\mathbf{e}) = 0 \qquad [6]$$

and:

$$\text{Var}\begin{bmatrix}\mathbf{Y}\\ \mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{ZZ}'\sigma_s^2 + \mathbf{R} & \mathbf{Z}\sigma_s^2 & \mathbf{R}\\ & \mathbf{I}\sigma_s^2 & 0\\ \text{Symmetric} & & \mathbf{R}\end{bmatrix} \qquad [7]$$

where σ_s^2 is the variance of transmitting abilities, and **R** is the residual variance-covariance matrix.

Each data set was analyzed with three models, which differed in the assumptions made regarding the form of **R**, as follows:

Model 1: $\mathbf{R} = \mathbf{I}\sigma_e^2$.

TABLE 1. *Effects of levels of fixed factors A and B, in units of standard deviation, and allocation of progeny to sire groups.*

		Progeny group									
Factor A	Factor B	1	2	3	4	5	6	7	. . .	50	Total
1.0	1.0	1	x	x	x	x	3	x	. . .	x	120
	.8	2	x	x	x	x	12	x	. . .	x	470
	.6	x	1	x	x	x	x	4	. . .	x	125
	.4	x	4	x	x	x	x	14	. . .	x	490
	.2	x	x	2	x	x	x	x	. . .	x	130
	0	x	x	6	x	x	x	x	. . .	x	510
	−.2	x	x	x	2	x	x	x	. . .	x	135
	−.4	x	x	x	8	x	x	x	. . .	x	530
	−.6	x	x	x	x	3	x	x	. . .	25	140
	−.8	x	x	x	x	10	x	x	. . .	100	550
−1.0	1.0	0	x	x	x	x	3	x	. . .	x	115
	.8	2	x	x	x	x	12	x	. . .	x	470
	.6	x	1	x	x	x	x	3	. . .	x	120
	.4	x	4	x	x	x	x	14	. . .	x	490
	.2	x	x	1	x	x	x	x	. . .	x	125
	0	x	x	6	x	x	x	x	. . .	x	510
	−.2	x	x	x	2	x	x	x	. . .	x	130
	−.4	x	x	x	8	x	x	x	. . .	x	530
	−.6	x	x	x	x	2	x	x	. . .	25	135
	−.8	x	x	x	x	10	x	x	. . .	100	550
		5	10	15	20	25	30	35	. . .	250	6375

Model 2: **R** = Diag $\{\sigma^2_{e_i}\}$, where i=1,2 indicates the two levels of factor A.

Model 3: **R** = Diag $\{\sigma^2_{e_{ij}}\}$, where i=1,2 and j=1, . . ., 10 indicate the levels of factors A and B.

In Model 2, the residual variance is heterogeneous with respect to levels of A, similar to the procedure described by Berger and Freeman (1). In Model 3, the residual variance is heterogeneous across A × B subclasses.

Transmitting abilities were estimated by the u-component of equations:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z+I\sigma_s^{-2} \end{bmatrix} \begin{bmatrix} \tilde{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}Y \\ Z'R^{-1}Y \end{bmatrix} \qquad [8]$$

with **R** differing across models as described.

Variance Components in the Categorical Scale

Theoretical results (6, 19) were used to approximate σ_s^2 and σ_e^2 needed in [8] from the known heritabilities and the expected incidence in the population. In theory:

$$\sigma_s^2 = \frac{h_Y^2}{4}\left[\sum_{i=1}^{m-1} z_i(a_{i+1}-a_i)\right]^2 \qquad [9]$$

and:

$$\sigma_Y^2 = \sum_{i=1}^{m} a_i^2 p_i - \left(\sum_{i=1}^{m} a_i p_i\right)^2 \qquad [10]$$

where σ_s^2 and σ_Y^2 are the "sire" and "total" variance components in the categorical scale, m is the number of categories of response (2 or 4), a_i is the "slope" for category i, p_i is the expected incidence in the i^{th} category, and z_i is the ordinate of the standard normal density function evaluated at the threshold between categories i and i+1. Because [9] and [10] strictly apply to models with a single fixed effect, contrived values were used to accommodate the layout considered in the present study. These were:

Model 1:

$$\tilde{\sigma}_s^2 = \sum_{i=1}^{2}\sum_{j=1}^{10}\frac{n_{ij}}{N}\,\sigma^2_{s_{ij}} \qquad [11]$$

$$\tilde{\sigma}^2_Y = \sum_{i=1}^{2}\sum_{j=1}^{10}\frac{n_{ij}}{N}\sigma^2_{Y_{ij}} \qquad [12]$$

$$\tilde{\sigma}^2_e = \tilde{\sigma}^2_Y - \tilde{\sigma}^2_s \qquad [13]$$

where n_{ij} is the number of records in the $A_i \times B_j$ subclass, N is the total number of observations, and $\sigma^2_{s_{ij}}$ and $\sigma^2_{Y_{ij}}$ are obtained by applying [9] and [10] to each of such subclasses.

Model 2:

$$\tilde{\sigma}^2_s = \text{as in Model 1} \qquad [14]$$

$$\tilde{\sigma}^2_{e_i} = \sigma^2_{Y_i} - \sigma^2_{s_i}$$

$$= \sum_{j=1}^{10}\frac{n_{ij}}{n_{i.}}(\sigma^2_{Y_{ij}} - \sigma^2_{s_{ij}});\ i=1,2 \qquad [15]$$

Model 3:

$$\tilde{\sigma}^2_s = \text{as in Model 1} \qquad [16]$$

$$\tilde{\sigma}^2_{e_{ij}} = \sigma^2_{Y_{ij}} - \sigma^2_{s_{ij}};\ i=1,2;\ j=1,\ldots,10 \qquad [17]$$

Note that a "pooled" sire variance component was used in all three models. However, [9] indicates this variance can potentially vary among fixed subclasses to the extent that incidences are heterogeneous across such subclasses. This illustrates, nonetheless, one of the difficulties in analyzing categorical data with linear models.

Comparison of Models

The analysis of each data set yielded three vectors of estimated transmitting abilities ($\hat{u}_1, \hat{u}_2, \hat{u}_3$) corresponding, respectively, to each of the three models used. The true transmitting abilities (**u**) were known from the simulation process. Because the main interest was in the ability of these models to rank sires correctly, rather than on biases or mean squared error of prediction, effectiveness of selection was the criterion chosen for comparison. Sires were ranked on the basis of $\hat{u}_1$, $\hat{u}_2$, and $\hat{u}_3$, and the average true transmitting ability of the 10 lowest ranking sires by each of the models was computed ($\bar{u}_{[1]}, \bar{u}_{[2]}, \bar{u}_{[3]}$); the brackets in the subscripts denote "selected". Because E(**u**) = **0**, then $\bar{u}_{[i]}$ (i=1,2,3) is a measure of effectiveness of truncation selection based on progeny test against "rare" categorical traits such as stillbirth in the binary case or calving difficulty when responses were tetrachotomous. The model yielding the largest response, averaged over replications, would be preferred. Differences between $\bar{u}_{[i]}$ and $\bar{u}_{[j]}$, $i \neq j$, were examined using paired t tests within each of the 12 experimental settings (underlying heritability × level of categorization); variance of the difference was estimated from the Monte Carlo replications. Results were also expressed in terms of the average relative efficiency of selection:

$$\text{ARE}_i = \frac{100}{R}\sum_{r=1}^{R}\frac{\bar{u}_{[i]}}{u_{[MIN]}};\ i=1,2,3 \qquad [18]$$

In [18], R is the number of replications, and $u_{[MIN]}$ is the average transmitting ability of the 10 sires with the lowest 10 true values. ARE_i would be maximal (100%) if the 10 sires ranking lowest in estimated and true transmitting ability were the same.

RESULTS

As shown in Table 2, realized responses to selection using the models allowing for heterogeneous variance (Models 2 and 3) were considerably and, in most instances, significantly lower than those obtained using the homoscedastic model (Model 1). The differences in terms of ARE were especially marked when responses were binary, particularly at lower incidence. For example, with h^2_y=.05 and 6.5% incidence, selection with Model 1 was two to three times more efficient than with the other models. With tetrachotomous responses, the differences between models were less marked and sometimes not significantly different from 0. When significant, the differences in ARE were of the order of 4 to 7% in favor of Model 1. The differences between Models 2 and 3 were generally not significantly different from 0. In summary, allowing for heterogeneity of residual variance as in Models 2 and 3 while maintaining the variance of transmitting ability constant, impaired the ability of BLUP to

TABLE 2. Average response (20 replicates) to progeny test selection (lower tail) upon evaluations with three mixed linear models.

h_y^2[1]	Incidence	h_c^2[2]	Response under model			Significance[3]			ARE[4]		
			1	2	3	1 vs. 2	1 vs. 3	2 vs. 3	1	2	3
	(%)								(%)		
.05	6.5	.022	−.647	−.339	−.294	***	***	NS	41.2	13.2	17.3
	15.1	.026	−.744	−.410	−.440	***	***	NS	54.6	31.2	33.1
	34.3	.027	−.770	−.693	−.642	NS	*	NS	55.5	50.1	47.0
	IV[5]	.039	−.815	−.733	−.765	NS	NS	NS	59.6	53.8	56.2
.20	6.5	.090	−.630	−.358	−.384	***	**	NS	43.4	23.4	25.3
	15.1	.105	−.924	−.654	−.695	***	***	NS	63.9	44.5	43.9
	34.3	.110	−1.173	−1.010	−.940	***	***	NS	79.8	67.9	62.9
	IV[5]	.158	−1.068	−1.010	−.982	*	*	NS	82.2	77.9	75.8
.50	6.5	.225	−.823	−.577	−.558	***	***	NS	58.8	40.1	38.7
	15.1	.262	−.914	−.676	−.599	***	***	*	71.7	54.2	48.5
	34.3	.274	−1.207	−1.064	−1.021	***	***	NS	82.8	72.4	69.1
	IV[5]	.394	−1.237	−1.169	−1.139	*	**	NS	88.7	83.9	81.5

[1] Heritability in underlying scale.

[2] Expected heritability in categorical scale.

[3] NS=$P > .05$; *=$.01 < P \leq .05$; **=$.001 \leq P < .01$; ***=$P \leq .001$.

[4] *Average relative efficiency. See equation (18).*

[5] Four categories of response (see text).

identify superior (inferior) sires for categorical traits.

PEVS were calculated for each of the three models from the diagonal elements of the sire × sire part of a generalized inverse of the coefficient matrix in [8]. For the situation where h_y^2=.05 and the expected incidence was 15.1%, PEV was plotted against progeny group size (varying from 5 to 250 in steps of 5) for each of the three models. This is shown in Figure 1 and the pattern is representative of what was observed in other settings. As in Berger and Freeman (1), allowing for heteroscedasticity clearly reduced "apparent" PEV. The "oscillatory" shape of the curve for Model 3 is due to disconnectedness between sires and levels of factor B. If the linear model in [3] were the "true" model and the "true" residual variances were as in Models 2 and 3, allowing for heteroscedasticity should have enhanced genetic progress, at least under normality (11). In this study, the "true" model was as in [1] and the relationship between genetic merit and the categorical responses is not linear (7, 8, 10, 14). Because of this, the reduction in PEV is "apparent" only, and the heteroscedastic models do not seem to improve the efficiency of selection attained with Model 1.

DISCUSSION

The properties of best linear unbiased prediction hold when the model is correct and when the needed variances and covariances (**R** and **G** with the latter being $\mathbf{I}\sigma_s^2$ in the present paper) are known, at least to proportionality (11, 12). If the errors have heterogeneous variance, **R** should be defined accordingly, i.e., heteroscedasticity should be incorporated into the model. Then, if σ_s^2 is homogeneous, heritability would be lower in the classifications having higher residual variance. The records in such classes would receive a smaller weight than those in classes with smaller σ_e^2 and would be "naturally" more strongly regressed toward the mean. This is well-known under linearity or, without loss of generality, normality.

If the threshold model is postulated, the genetic variance in the categorical scale is not independent of the fixed effects (2, 3, 6, 7, 8, 10, 19), a situation that has been observed

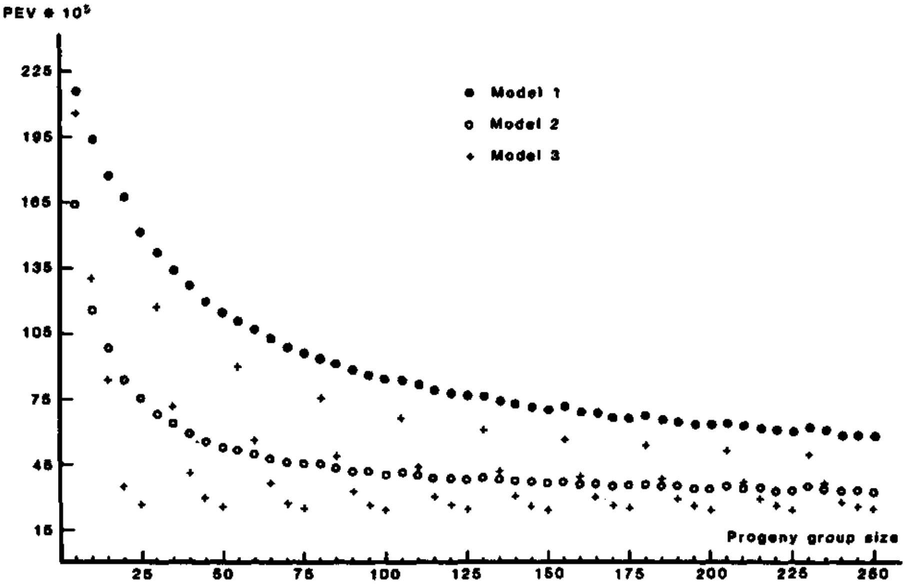

Figure 1. Prediction error variance (PEV) calculated from models, 1, 2, and 3 assuming $h_y^2=.20$ (heritability of liability) and an expected incidence of 15.1%.

in field records (1) and supported by simulation studies (15, 18). With binary responses (8), the variance of transmitting abilities in the categorical scale can be written as:

$$\sigma_s^2 = \frac{h^2}{4}\,\phi^2(t-\mu_j) \qquad [19]$$

where $\phi(.)$ is the standard normal density function, and $t\text{-}\mu_j$ is the distance between the threshold (t) and a parameter (μ_j) in the underlying scale. Clearly [19] depends on μ_j; it is maximum when $t=\mu_j$ (50% incidence) and declines as the incidence deviates from 50%. The dependency of [19] on μ_j illustrates a serious conceptual problem in analysis of categorical responses via linear models: the covariance between two half-sibs depends on the μ_j values, which include a component pertaining to the conditions under which the sibs produced their records and a component due to the transmitting ability of their sire (7, 8, 10). Consequently, G cannot be defined without reference to $\underset{\sim}{\beta}$ and u in [8], a situation that does not occur under normal distribution theory. Also, arguing from the threshold model, the residual variance in the j^{th} subclass is $\Phi(t-\mu_j)\,[1-\Phi(t-\mu_j)]$ (7, 8, 10), where Φ (.) is the standard normal distribution function. Hence, the variance ratio σ_e^2/σ_s^2 in the observable scale varies from subclass to subclass, being minimal when $t=\mu_j$ (incidence in the subclass equal to 50%), at which point there should be less regression than at other incidences. However, if σ_s^2 is kept constant for linear analysis, then there is more regression when the incidence is 50% than at other incidences, the reason being that at this point residual variance is maximum. Hence, allowing for heteroscdeastic residual variance while keeping a constant "sire" variance in a mixed linear model analysis for categorical data does exactly the opposite of what it should do! It is, therefore, not surprising that Models 2 and 3 were less able to identify superior (inferior) sires than Model 1 under the conditions considered in this paper.

CONCLUSION

The results of the simulation study suggest that the ability of BLUP to rank sires for categorical traits is impaired by ad hoc "adjustments" for heteroscedasticity, particularly when responses are binary. This is consistent with deductions from the theory of threshold models. If investigators choose to evaluate sires for categorical responses with linear rather than with nonlinear methods, homoscedastic models seem more robust than heteroscedastic ones, at least within the range of conditions studied here. In many instances, especially with polychotomous responses, differences in sire rankings obtained with nonlinear and linear homoscedastic mixed models are negligible for practical purposes (14).

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Chapter 4

Sire evaluation for calving traits by Best Linear Unbiased Prediction and nonlinear methodology

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Research Institute for Animal Production „Schoonoord", Zeist, The Netherlands

Sire evaluation for calving traits by Best Linear Unbiased Prediction and nonlinear methodology

By A. Meijering

Ms. received 20. 9. 1984

Introduction

It has been established that bulls as sires of calves may differ considerably in dystocia and stillbirth rate at birth of their progeny (e. g. Meijering 1984). Sire evaluation programs for these traits, based on progeny tests, have been introduced in many European countries (Philipsson et al. 1979) as well as in the U. S. (Thompson et al. 1980) and in Canada (Cady and Burnside 1982). At best, genetic merits are predicted by the method of Best Linear Unbiased Prediction (BLUP). From a distributional viewpoint however, a linear approach is hard to justify with categorical variates (Thompson 1979; Gianola 1980, 1982). Among the problems encountered are heteroscedasticity of sire and error variances, and arbitrariness in assigning scores to the response categories of polychotomous variates (Gianola 1980, 1982). Also, important properties of BLUP, i. e. Maximum Likelihood estimation of the Best Predictor and maximization of the probability of correct pairwise ranking, are only derived under the assumption of multivariate normality of data and genetic merits to be predicted (Henderson 1973). With categorical variates this assumption is not met, and then Best Linear Predictors may not maximize the probability of correct ordering (Gianola 1980; Portnoy 1982).

Because of the theoretical inadequacy of the linear model when variates are categorical, Gianola and Foulley (1983) proposed a nonlinear method (GFCAT) of sire evaluation for ordered polychotomous traits, based on the threshold concept (e. g. Falconer 1983) and Bayes' theorem. A similar procedure was suggested by Harville and Mee (1982). In a simulation study (Meijering and Gianola 1984) the ranking properties of GFCAT proved to be significantly superior in a mixed model setting with binary data under certain parameter conditions (incidence below 25 %; moderate to high heritability ($h^2 \geqq 0.20$) in the underlying scale). Under other conditions, and with tetrachotomous data, BLUP and GFCAT yielded equivalent results.

It is of course virtually impossible to mimic the full complexity of a field data set in a simulation study. The main objective of the present paper is to examine the practical relevance of differences in ranking properties between BLUP and GFCAT for the future sire evaluation procedure in The Netherlands birth recording program.

Material and methods

Data

The data set used contained progeny test records for calving traits (dystocia, stillbirth, gestation length, birth weight) from unproven Friesian bulls (< 50 % Holstein genes) collec-

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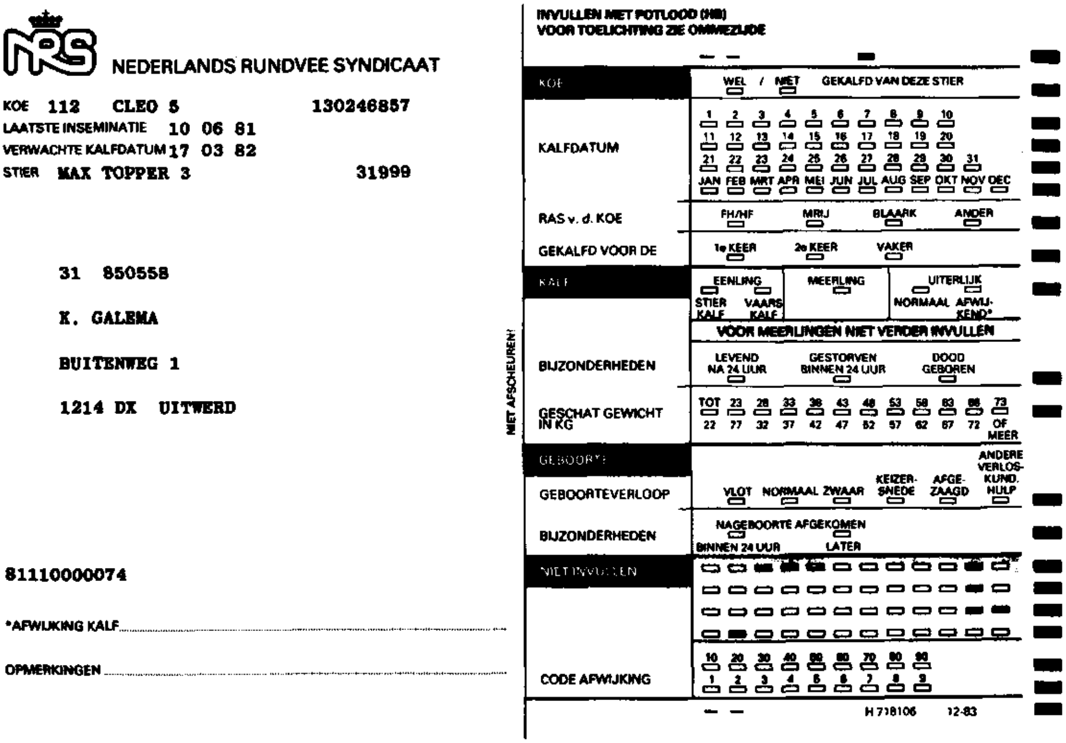

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GEKALFD VOOR DE	1e KEER ☐ 2e KEER ☐ VAKER ☐
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Fig. 1. Mark sense card used in the Netherlands birth recording program

ted by a major A. I. organization (Zuid West Nederland) from January 1980 to June 1982. A record consisted of herd and sire identifications, breeding and calving dates, information on breed and parity of dam and number and sex of calves, codes for presentation, congenital defects (if any) and viability, a score for difficulty of parturition, and an estimate of birth weight. Herdsmen supplied this information on mark-sense cards (figure 1). These had been forwarded to them around the expected time of calving, carrying sire and dam identifications and breeding and expected calving dates: a standard procedure in the birth recording program. Birth weight was estimated in multiples of 5 kg. Viability was classified as (1) alive or (2) dead within 24 hr of birth. Difficulty of parturition was scored as: (1) easy = no or minor assistance, (2) normal = easy pull, (3) difficult = hard pull or veterinary aid, (4) Caesarean or fetotomy (PHILIPSSON et al. 1979). In The Netherlands, as a rule, unproven bulls are mated to first lactation heifers. Thus a vast majority of the records referred to second calvings. Only these records were used. After editing for incomplete records, non-Friesian dams, twins, malpresentations, congenital morphological defects and extreme gestation length ($<$ 261 or $>$ 299 days), 18218 records of 77 sires across 2055 herds were available. The number of progeny per sire was between 121 and 400, averaging 236.6. The structure of the data set may be considered representative for the national birth recording program.

Methods

Apart from parity and sire, calving traits are generally found to be affected by sex of calf, herd and season of calving (e. g. POLLAK and FREEMAN 1976; MEIJERING 1984). Herd effects on dystocia account for systematic differences among herdsmen in both handling parturition and scoring its degree of difficulty. As season classes are not well defined, a preliminary analysis was done by the following simple fixed model (HARVEY 1977):

$$Y_{ijk} = \mu + ym_i + g_j + e_{ijk} \tag{1}$$

where

y_{ijk} = observation on calf k of sex j born in year-month i
μ = constant common to all records
ym_i = effect of year-month i (i = Jan. 1980 ... June 1982)
g_j = effect of sex j (j = 1, 2)
e_{ijk} = residual
$E(e_{ijk})$ = 0
$E(e^2_{ijk})$ = σ^2_e
$E(e_{ijk}, e_{ijk'})$ = 0, $k \neq k'$

Based on the year-month estimates obtained (figure 2) and the relatively small number of observations per herd, it was decided to construct herd-season (HS) classes instead of the more common herd-year-season (HYS) classes. A season was defined as a six month period (Jan.–June; July–Dec.). Thus 3412 HS-classes, 681 with a single observation, were obtained.

BLUP-solutions and variance components were estimated simultaneously by the iterative procedure proposed by SCHAEFFER and BURNSIDE (1974). Herein variance components are estimated by an iterative version of MINQUE. The data were modeled as:

$$\underset{\sim}{y} = \underset{\sim}{X}_1\underset{\sim}{h} + \underset{\sim}{X}_2\underset{\sim}{g} + \underset{\sim}{Z}\underset{\sim}{u} + \underset{\sim}{e} \tag{2}$$

, where

$\underset{\sim}{y}$ = vector of 18218 observations;
$\underset{\sim}{h}$ = vector of 3412 herd-season classes;
$\underset{\sim}{g}$ = vector of sex effects;
$\underset{\sim}{u}$ = vector of 77 sire values to be predicted;
$\underset{\sim}{e}$ = 18218 × 1 vector of residuals;
$\underset{\sim}{X}_1, \underset{\sim}{X}_2, \underset{\sim}{Z}$ = known incidence matrices of appropriate order.

Assumptions on location and dispersion were:

$$E\begin{bmatrix}\underset{\sim}{y}\\ \underset{\sim}{u}\\ \underset{\sim}{e}\end{bmatrix} = \begin{bmatrix}\underset{\sim}{X}_1\underset{\sim}{h} + \underset{\sim}{X}_2\underset{\sim}{g}\\ \underset{\sim}{0}\\ \underset{\sim}{0}\end{bmatrix} \qquad \mathrm{Var}\begin{bmatrix}\underset{\sim}{y}\\ \underset{\sim}{u}\\ \underset{\sim}{e}\end{bmatrix} = \begin{bmatrix}\underset{\sim}{Z}\underset{\sim}{Z}'\sigma^2_s + \underset{\sim}{I}_e\sigma^2_e & \underset{\sim}{Z}\,\sigma^2_s & \underset{\sim}{I}_e\sigma^2_e\\ & \underset{\sim}{I}_s\sigma^2_s & \underset{\sim}{0}\\ \text{symmetric} & & \underset{\sim}{I}_e\sigma^2_e\end{bmatrix}$$

After absorption of herd-seasons the mixed model equations were:

$$\begin{bmatrix}\underset{\sim}{X}_2'\underset{\sim}{S}\underset{\sim}{X}_2 & \underset{\sim}{X}_2'\underset{\sim}{S}\underset{\sim}{Z}\\ \underset{\sim}{Z}'\underset{\sim}{S}\underset{\sim}{X}_2 & \underset{\sim}{Z}'\underset{\sim}{S}\underset{\sim}{Z} + \underset{\sim}{I}_s\alpha^{[i]}\end{bmatrix}\begin{bmatrix}\hat{\underset{\sim}{g}}^{[i+1]}\\ \hat{\underset{\sim}{u}}^{[i+1]}\end{bmatrix} = \begin{bmatrix}\underset{\sim}{X}_2'\underset{\sim}{S}\underset{\sim}{y}\\ \underset{\sim}{Z}'\underset{\sim}{S}\underset{\sim}{y}\end{bmatrix}$$

where i = round of iteration, $\underset{\sim}{S} = \underset{\sim}{I} - \underset{\sim}{X}_1(\underset{\sim}{X}'_1\underset{\sim}{X}_1)^{-1}\underset{\sim}{X}'_1$ and $\alpha^{[i]} = \hat{\sigma}^{2[i]}_e/\hat{\sigma}^{2[i]}_s$

A generalized inverse was obtained by setting the solution for sex 1 to zero. Variance components at round i + 1 were estimated from the equations:

$$\begin{bmatrix}s - 2c_1\hat{\alpha}^{[i]} + c_2\,\hat{\alpha}^{2[i]} & c_1 - c_2\,\hat{\alpha}^{[i]}\\ \hat{\alpha}^{2[i]}\,(c_1 - c_2\,\hat{\alpha}^{[i]}) & N-h-r+c_2\,\hat{\alpha}^{2[i]}\end{bmatrix}\begin{bmatrix}\hat{\sigma}^{2[i+1]}_s\\ \hat{\sigma}^{2[i+1]}_e\end{bmatrix}$$

$$= \begin{bmatrix}\hat{\underset{\sim}{u}}'^{[i+1]}\,\hat{\underset{\sim}{u}}^{[i+1]}\\ \underset{\sim}{y}'\underset{\sim}{S}\underset{\sim}{y} - \hat{\underset{\sim}{g}}'^{[i+1]}\underset{\sim}{X}_2'\underset{\sim}{S}\underset{\sim}{y} - \hat{\underset{\sim}{u}}'^{[i+1]}\underset{\sim}{Z}'\underset{\sim}{S}\underset{\sim}{y} - \hat{\underset{\sim}{u}}^{[i+1]}\hat{\underset{\sim}{u}}^{[i+1]}\hat{\alpha}^{[i]}\end{bmatrix}$$

, where c_1 = trace of the sire part ($\underset{\sim}{T}_{22}$) of the inverted coefficient matrix $\underset{\sim}{T}$; c_2 = sum of squared elements of $\underset{\sim}{T}_{22}$; s = number of sires; h = number of herd-seasons; N = number of observations; r = rank of the coefficient matrix. Sire components of covariance were estimated analogously, by summation of traits:

$$\hat{\sigma}_{s_j s_k} = \tfrac{1}{2}(\hat{\sigma}^2_{s_{(j+k)}} - \hat{\sigma}^2_{s_j} - \hat{\sigma}^2_{s_k}),$$ where j and k indicate different traits.

Iteration was terminated when $1 - \frac{\alpha^{[i+1]}}{\alpha^{[i]}} < 0.01$. Two very divergent sets of starting values for $\alpha^{[0]}$ were examined, which however led to the same solutions in at most six rounds of iteration.

Evaluation by the nonlinear method was limited to the traits dystocia and stillbirth. Strictly speaking however, birth weight could also be considered categorical here. Although not essential, the data were rearranged into contingency tables of order p × m, where the p rows represented specific combinations of herd-season, sex and sire with totals assumed fixed, and the m columns were categories of response (m = 4 for dystocia and m = 2 for stillbirth).

Assuming and underlying normally distributed 'liability' variate responding in the observable scale through a set of m − 1 fixed thresholds ($t_1 \ldots t_{m-1}$ with $t_0 = -\infty$ and $t_m = +\infty$), the liability of the a^{th} observation in the j^{th} row can be written as:

$$l_{jq} = \eta_j + \varepsilon_{jq}, \text{ with } \varepsilon_{jq} \sim \text{IID } N(0, 1) \text{ and } \eta_j = \text{location parameter for row } j.$$

The p × 1 vector of location parameters was modeled as:

$\underset{\sim}{\eta} = \underset{\sim}{X}_1\underset{\sim}{h} + \underset{\sim}{X}_2\underset{\sim}{g} + \underset{\sim}{Z}\underset{\sim}{u}$, where $\underset{\sim}{h}$, $\underset{\sim}{g}$ and $\underset{\sim}{u}$ are the parameter vectors specified for model (2), and $\underset{\sim}{X}_1$, $\underset{\sim}{X}_2$ and $\underset{\sim}{Z}$ are known incidence matrices of appropriate order, indicating the presence of particular herd-seasons, sexes and sires in the row combinations.

Given the location parameter, the probability of response in the k^{th} category for observation q in row j is then:

$$\begin{aligned} P_{jk} = \text{Prob}\,\{t_{k-1} < \ell_{jq} < t_k \mid \eta_j\} &= \Phi[t_k - (\underset{\sim}{x}'_{1j}\underset{\sim}{h} + \underset{\sim}{x}'_{2j}\underset{\sim}{g} + \underset{\sim}{z}'_j\underset{\sim}{u})] \\ &\quad - \Phi[t_{k-1} - (\underset{\sim}{x}'_{1j}\underset{\sim}{h} + \underset{\sim}{x}'_{2j}\underset{\sim}{g} + \underset{\sim}{z}'_j\underset{\sim}{u})] \end{aligned} \qquad (3)$$

, where Φ [.] denotes the normal integral.

The data are assumed to follow the product multinomial distribution, the likelihood function being:

$$g(\underset{\sim}{y} \mid \underset{\sim}{t}, \underset{\sim}{h}, \underset{\sim}{g}, \underset{\sim}{u}) = \prod_j \left[\frac{n_{j.}!}{\prod_k n_{jk}!} \prod_k P_{jk}{}^{n_{jk}} \right] \quad (j=1 \ldots p;\ k=1 \ldots m)$$

, where $n_{j.}$ = total of row j, n_{jk} = k^{th} subcell total in row j; P_{jk} is as defined in (3).

Prior information on $\underset{\sim}{t}$, $\underset{\sim}{h}$ and $\underset{\sim}{g}$ was assumed to be vague. The distribution of $\underset{\sim}{u}$ was assumed normal with expectation zero and covariance $\underset{\sim}{I}\sigma^2_s$. Following Bayes' theorem the log-posterior density is proportional to:

$$L(\underset{\sim}{t}, \underset{\sim}{h}, \underset{\sim}{g}, \underset{\sim}{u} \mid \underset{\sim}{y}) \propto \sum_{j=1}^{p} \sum_{k=1}^{m} n_{jk} \ln(P_{jk}) - (\underset{\sim}{u}'\underset{\sim}{u}/2\sigma^2_s)$$

, where P_{jk} is again as defined in (3).

As suggested by GIANOLA and FOULLEY (1983), the mode of the posterior density was taken as an approximation to the Best Predictor, and the parameter vector, $\underset{\sim}{\theta}' = [\underset{\sim}{t}', \underset{\sim}{h}', \underset{\sim}{g}', \underset{\sim}{u}']$ was estimated iteratively by a modification of the Newton-Raphson method:

$$-E\left[\frac{\partial^2 L}{\partial\underset{\sim}{\theta}\partial\underset{\sim}{\theta}'}\right]^{[i-1]} \left[\underset{\sim}{\theta}^{[i]} - \underset{\sim}{\theta}^{[i-1]}\right] = \left[\frac{\partial L}{\partial\underset{\sim}{\theta}}\right]^{[i-1]}$$

An extensive derivation of the final equations was given by Gianola and Foulley (1983).

Before setting up the equations a check was made for herd-seasons with all responses in an extreme category (category 1 or m). Combinations made up of these herd-seasons were removed from the contingency table as otherwise the system of equations will not converge (Harville and Mee 1982): the solutions for these herd-seasons will tend to plus or minus infinity. Deleting these combination will not affect the sire solutions. A similar procedure should be followed for other fixed effects in the model. This however did not lead to additional deletions here. The number of herd-seasons was reduced to 2833 for dystocia and to 492 for stillbirth with 17100 and 4076 observations, respectively. The solutions for herd 1 and sex 1 were set to zero to obtain full rank for the matrix of second partials. Starting values for all parameters were zero, except for the thresholds in the evaluation for dystocia, which were $t_1^{[o]} = 0$, $t_2^{[0]} = 1$ and $t_3^{[0]} = 2$. Sire variances in the underlying scale ($\sigma^2_e = 1$) were derived from the heritability estimates obtained in the linear model analysis: $\sigma^2_s = \hat{h}^2/(4 - \hat{h}^2)$.

Operationally the herd-season equations were absorbed into the equations for threshold(s), sex and sires at each round of iteration. The resulting matrix of order 79 for stillbirth and 81 for dystocia was inverted directly. Subsequently herd-season estimates were obtained by backsolution. Iteration was terminated when the differences between successive estimates were less than 10^{-4} for threshold(s), sex and sires, and less than 10^{-2} for herd-seasons.

Results and discussion

Overall means and standard deviations are given in table 1. The means and frequencies are consistent with earlier findings in similar data sets (Meijering and Van Eldik 1981). The overall classification of calving ease was: 43.8% easy, 48.4% normal, 7.4% difficult and 0.4% Caesarean/fetotomy.

Table 1. **Overall means and standard deviations (s. d.)**

trait	mean	s.d.
dystocia score	1.64	0.63
stillbirth (%)	2.72	1.63
birth weight (kg)	37.46	5.05
gestation length (d)	278.49	4.98

The year-month estimates shown in figure 2 supply additional evidence for the existence of a seasonal pattern, in particular for birth weight and dystocia, with peaks in the fall, as discussed earlier (Meijering 1984). The low and high values at the beginning and the end of the sampling period, respectively, have to be considered as artefacts due to predominant sampling from the early born progeny from the first groups and the late born progeny from the last groups represented in the data set, respectively.

Heritability and genetic correlation estimates are given in table 2. The heritability estimates are within the ranges given by Philipsson et al. (1979). The estimate for birth weight is close to the lower bound of the expected range. This result may have been caused by the way of recording. Except where stillbirth is involved, the genetic correlation estimates are consistent with previous findings (Philipsson et al. 1979; Meijering 1984), confirming the very strong additive genetic relationship between dystocia and birth weight. The extremely low heritability estimate for stillbirth and the genetic correlation estimates out of parameter space when this trait is involved, may have a common cause. The variance components were estimated by a quasi MINQUE procedure. The estimates do not have true MINQUE properties because they are the result of iterations (Schaeffer and Burnside 1974). It is to be expected however, that the properties of MINQUE, i.e. unbiasedness and translation invariance, do not hold with categorical variates. Although distribution independent, MIN-

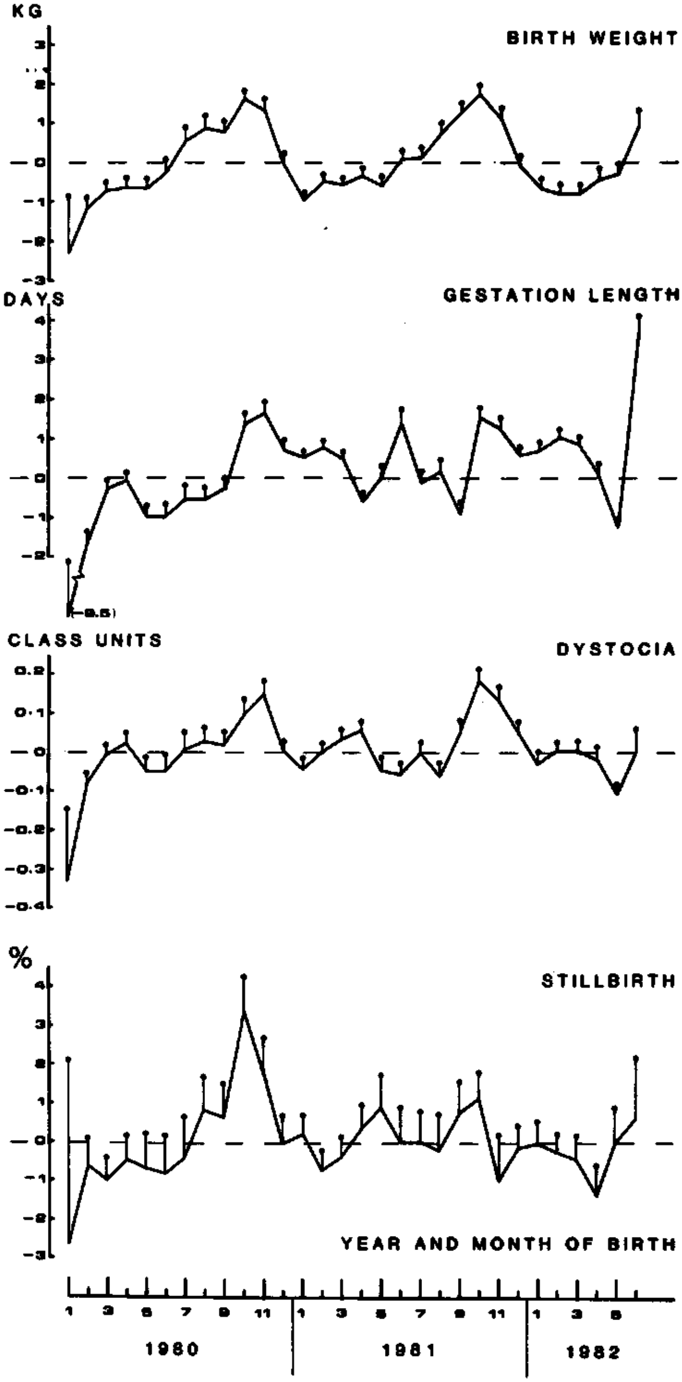

Fig. 2. Year-month estimates with standard errors, as obtained by model (1)

QUE was developed from an additive linear model (RAO 1973). This type of model is likely to yield underestimated heritabilities and sire components of variance for categorical traits (e.g. VINSON et al. 1976; GIANOLA 1980, 1982), and in particular for binary traits with low incidence. The behaviour of variance components for sums of categorical, or categorical and continuous, variates is rather unpredictable. Subtraction of underestimated components of variance for single traits from the sum component is likely to yield overestimated components of covariance however, and consequently overestimated genetic correlations. For the comparison of linear and nonlinear methods of sire evaluation to be entirely correct, sire variance components to be applied in the nonlinear procedure have to be estimated in the underlying scale. However, theory in this field is limited as yet. A first suggestion, an iterative algorithm to be viewed as an extension of restricted maximum likelihood (REML) was made by HARVILLE and MEE (1982).

The conditions for convergence in GFCAT were met after 8 and 6 rounds of iteration for dystocia and stillbirth, respectively. In spite of rapid convergence, the method was compu-

Table 2. **Estimates of heritabilities (diagonal) and genetic correlations**

	(1)	(2)	(3)	(4)
dystocia score (1)	0.093	1.755	0.889	0.541
stillbirth (2)		0.003	1.752	1.196
birth weight (3)			0.129	0.420
gestation length (4)				0.458

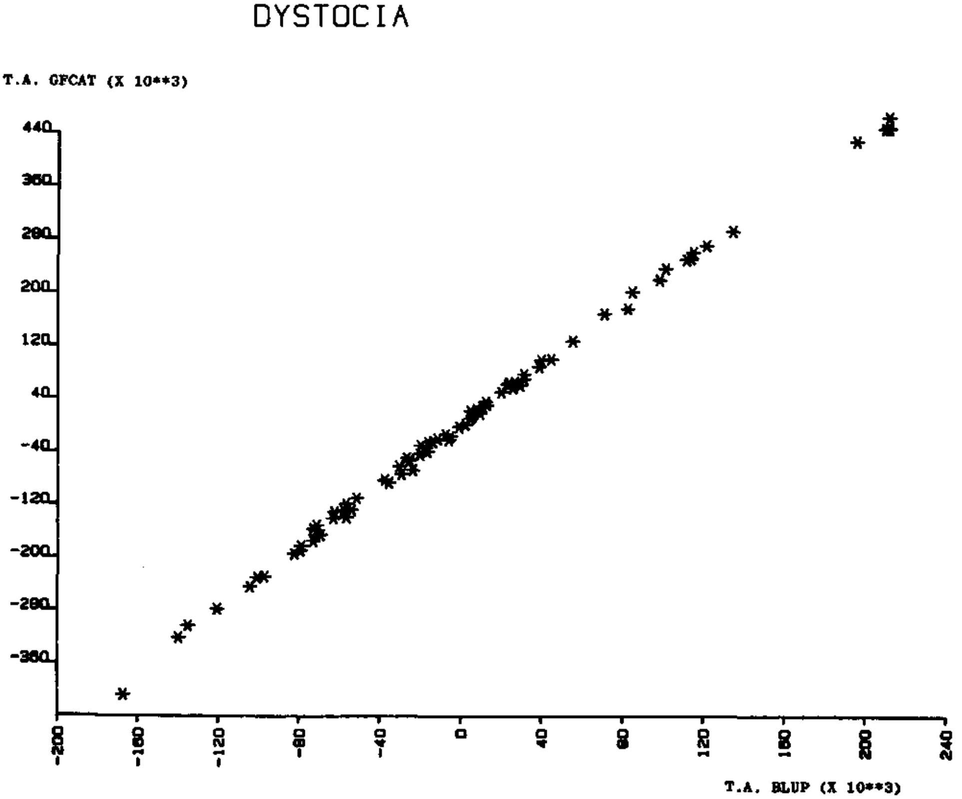

Fig. 3. Transmitting ability (T. A.) estimates for dystocia by BLUP and GFCAT

Fig. 4. Transmitting ability (T. A.) estimates for stillbirth by BLUP and GFCAT

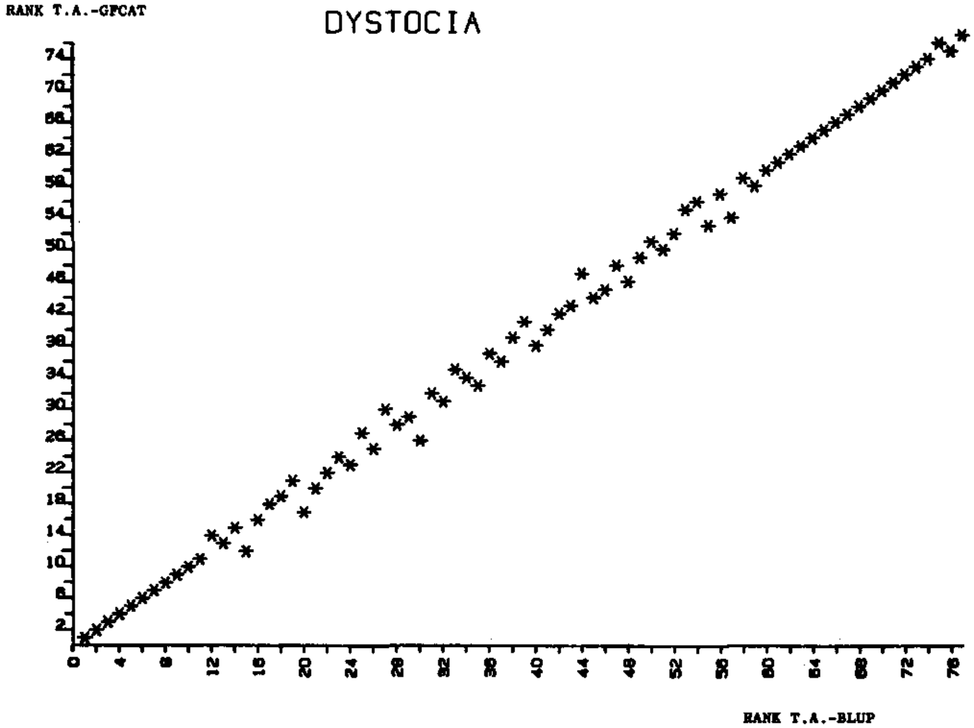

Fig. 5. Plot of sire ranking on transmitting ability (T. A.) estimates for dystocia by BLUP and GFCAT

tationally very expensive, mainly because of the repeated absorption and backsolution of herd-season equations. For the method to be applicable in regular sire evaluation at acceptable expense, speeding up procedures should be studied. The sire solutions (estimated transmitting abilities) obtained are plotted against the BLUP-solutions in figure 3 for dystocia and in figure 4 for stillbirth. Rankit plots are given in figures 5 and 6. For both traits the solutions were very highly correlated (r ≅ 0.99). Because they are on a different scale the solutions are not directly comparable in the absolute sense. For dystocia the methods show only minor differences in sire ranking (figure 5), which is consistent with the results of a simulation study (Meijering and Gianola 1984). Differences in ranking for stillbirth are somewhat more pronounced, but mainly located around the centre of the distribution of genetic merits and therefore of minor importance for selection of sires. Moreover it is questionable whether sire evaluation is worth the effort at all in the present situation, considering the extremely small sire variance. For, even if heritability was three times as high as estimated here, indirect selection through dystocia would be as efficient as direct selection for stillbirth with the present effective progeny group sizes (98–310) and a genetic correlation between 0.6 and 0.8.

When comparing different methods of evaluation, one should realize that the results are subject to the qualities of the data set used. Here, the data set was very robust and not extremely variable in effective number of progeny per sire. In such a setting BLUP is obviously equivalent to GFCAT for both a tetrachotomous trait and a binary trait with low incidence and heritability. Thus, in the Netherlands birth recording program there is no advantage in applying the theoretically better justifyable, but relatively expensive, GFCAT procedure. Under other conditions (lower and more variable numbers of progeny) there might be an advantage, at least with binary traits (Meijering and Gianola 1984).

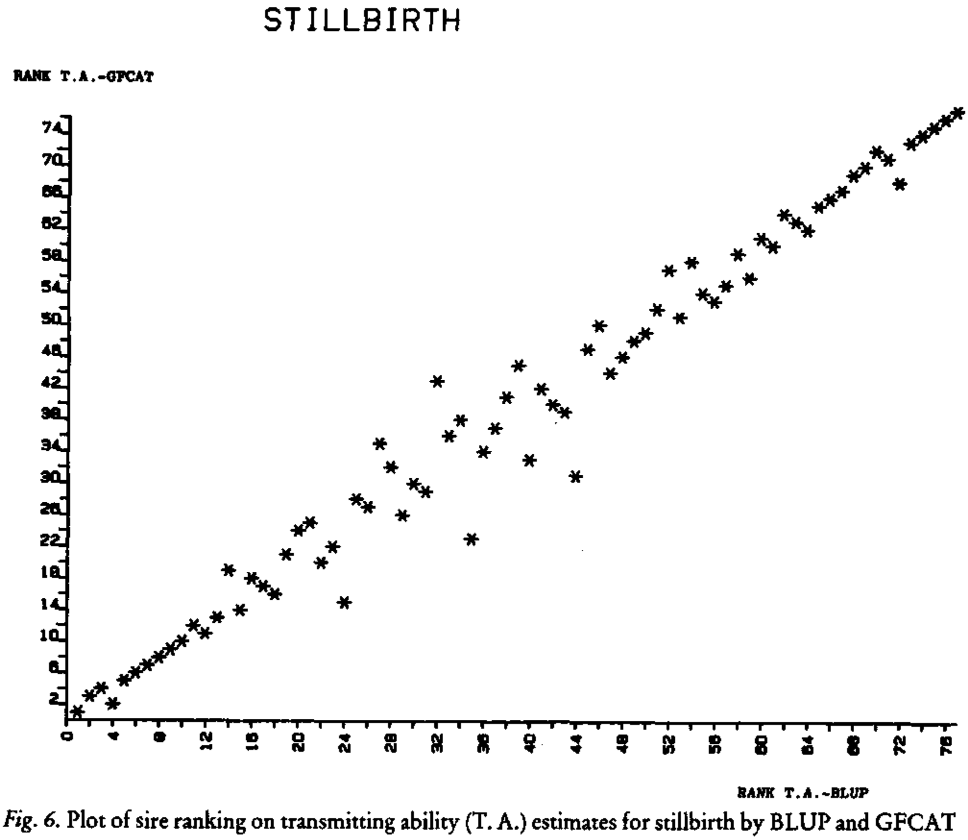

Fig. 6. Plot of sire ranking on transmitting ability (T. A.) estimates for stillbirth by BLUP and GFCAT

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Summary

A linear (BLUP) and a nonlinear (GFCAT; Gianola and Foulley, 1983) method of sire evaluation were compared in estimating genetic merits for dystocia (4 categories) and stillbirth (2 categories) with a field data sample from the birth recording program in The Netherlands. Data for 77 Friesian sires with 18218 progeny across 2055 herds were available. BLUP-solutions and variance components, for dystocia, stillbirth, birth weight and gestation length, were obtained simultaneously by an iterative procedure proposed by Schaeffer and Burnside (1974). Covariance components were estimated analogously, by summing traits. Heritabilities and most genetic correlations were within the ranges to be expected from earlier reports. However, heritability for stillbirth was extremely low and the genetic correlation estimates were out of the parameter space when this trait was involved. Sire solutions obtained by BLUP and GFCAT were very highly correlated (r ~ 0.99) for dystocia as well as for stillbirth. Only minor differences in sire ranking were observed, mainly around the centre of the distribution of genetic merits. The dependence of these results on the qualities of the data set is discussed. It is concluded that there is no major advantage in applying GFCAT under the conditions of the national birth recording program in The Netherlands.

Zusammenfassung

Zuchtwertschätzung für Abkalbemerkmale mittels BLUP und nicht-linearer Methodik

Eine lineare (BLUP) und eine nicht-lineare (GFCAT, Gianola und Foulley 1983) Methode der Bullenbewertung wurden bei der Zuchtwertschätzung für die kategorischen Merkmale Schwergeburt (4 Stufen) und Totgeburt (2 Stufen) in einer Felddatenprobe aus dem niederländischen Geburtsmeldeprogramm verglichen. Daten von 77 schwarzbunten Bullen mit 18218 Kälbern in 2055 Betrieben wurden verwendet. BLUP-Lösungen und Varianzkomponenten für Schwergeburt, Totgeburt sowie Geburtsgewicht und Tragezeit wurden gleichzeitig mittels einer iterativen Methode geschätzt. Kovarianzkomponente wurden auf ähnliche Weise durch Addierung der Merkmalswerte geschätzt.

Die Heritabilitäten und die Mehrzahl der genetischen Korrelationen lagen innerhalb des auf Grund früherer Beiträge erwarteten Bereiches. Die Heritabilität für Totgeburt war jedoch sehr niedrig und die Schätzwerte der genetischen Korrelation lagen außerhalb des Parameterraumes, wenn dieses Merkmal einbezogen war.

Die BLUP- und GFCAT-Lösungen waren sehr hoch korreliert (r ≅ 0,99) für Schwergeburt wie auch für Totgeburt. Für beide Merkmale ergaben sich nur geringfügige Unterschiede in der Reihenfolge der Bullen, die außerdem überwiegend in der Nähe des Zentrums der Schätzwerteverteilung lokalisiert waren. Die Abhängigkeit der Resultate von der Struktur des Datenbestandes wird diskutiert.

Es wird gefolgert, daß die Verwendung von GFCAT unter den Bedingungen des niederländischen Geburtsmeldeprogrammes keine klaren Vorteile bietet.

Résumé

Estimation de la valeur héréditaire moyennant BLUP et méthodologie non-linéaire pour les caractéristiques de vêlage

Une méthode linéaire (BLUP) et non-linéaire (GFCAT, Gianola et Foulley 1983) de l'évaluation dees taureaux ont été comparées dans l'estimation de la valeur héréditaire pour les caractères catégoriques dystocie (4 catégories) et mortinatalité (2 catégories) avec un échantillon des dates de champs du programme de notification de naissance aux Pays-Bas. Les dates de 77 taureaux pie-noire avec 18218 veaux en 2055 troupeaux étaient disponibles. Les solutions BLUP et composantes de la variance, pour dystocie, mortinatalité ainsi que poids à la naissance et durée de gestation étaient obtenus simultanément par un procédé itératif proposé par Schaeffer et Burnside (1974). Les composantes de la covariance étaient estimées de manière analogue par addition des valeurs des signes caractéristiques. Les héritabilités et la plupart des corrélations génétiques étaient au-dedans des domaines supposés de rapports antérieurs. Cependant, l'héritabilité pour mortinatalité était extrêmement basse et les valeurs estimatives des corrélations génétiques étaient au-dehors de l'espace des paramètres lorsque ce caractère était inclus. Les solutions BLUP et GFCAT étaient très hautement corrélés (r ≅ 0.99) pour dystocie aussi bien que pour mortinatalité. Des différences insignifiantes s'observaient seulement dans l'ordre de priorité des taureaux, principalement localisées autour du centre de distribution des valeurs estimatives. La dépendance de ces résultats sur les qualités de la partie intégrante des dates est discutée. On en conclut qu'il n'y a pas d'avantage majeur par l'application de GFCAT sous les conditions du programme de notification de naissance aux Pays-Bas.

Resumen

Estimación del Valor de Cría mediante BLUP y métodologia no líneal para características en el parto.

Un método líneal (BLUP) y no líneal (GFCAT, GIANOLA y FOULLEY 1983) en la evaluación paterna, fueron comparados en la estimación del mérito genético de Dístocia (4 Categorías) y Nacidos Muertos (2 Categorías) en una muestra a partir de datos de campo desde el Programa de Registro de Nacimiento en Holanda.

Fueron disponibles datos de 77 padres Friesien, con 18218 progenies en 2055 rebaños. Fueron obtenidas simultaneamente por un procedimiento iterativo propuesto por Schaeffer y Burnside (1974), las soluciones BLUP y componentes de varianzas para Dístocia, nacidos muertos, peso al nacimiento y largo de gestación. Análogamente fueron estimados los componentes de Covarianzas mediante adición de las características. Las heredibilidades y la mayoría de las correlaciones genéticas desde registros tempranos estuvieron dentro de los rangos esperados. Sin embargo, la heredabilidad para nacidos muertos fue extremadamente pequeña y las correlaciones genéticas estimadas yacen fuera del espacio parametral, cuando esta característica fue involucrada. Las soluciones obtenidas mediante BLUP y GFCAT fueron muy altamente correlacionadas ($r \sim 0.99$) para Dístocia y así como también nacidos muertos. Solamente leves diferencias fueron observadas en el orden de los padres, principalmente ubicados alrededor del centro de la distribución de los méritos genéticos. Se discute la dependencia de estos resultados sobre la calidad de esta serie de datos. Se concluye que el uso del GFCAT bajo las condiciones del Programa de Registro de Nacimiento holandes, no ofrece mayores ventajas.

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Part III

STUDIES ON SOME ASPECTS OF SIRE SELECTION FOR DYSTOCIA

Chapter 5

Morphologic aspects of dystocia in dairy and dual purpose heifers

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MORPHOLOGIC ASPECTS OF DYSTOCIA IN DAIRY AND DUAL PURPOSE HEIFERS

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The phenotypic association between ease of calving and a number of, mainly morphologic, dam traits was examined by stepwise discriminant analysis. Body weight, body dimensions and scores for fat covering and muscularity were obtained for 79 Holstein (H), 90 Dutch Red and White (DRW) and 104 Dutch Friesian (DF) heifers at 10 days after calving, Dimensions were body length, height at hips and withers, width and depth of chest, heart girth, hip width and spiral girth. About half of the heifers had data on precalving pelvic dimensions, both internal (height and width of pelvic inlet) and external (width at hips and thurls, pinbone distance, horizontal and vertical distances between hip and thurl, and hip and pinbone). Birth weight of all, and body dimensions of live calves were recorded. Calving ease was scored as 'easy' (no or minor assistance), 'normal' (easy pull) or 'difficult' (hard pull or Caesarean). In addition, forces exerted by a calf puller were recorded in a number of easy, normal and difficult deliveries. Analysis of these forces indicated that classification as 'easy' vs. 'normal' was more influenced by subjectivity or chance than 'normal' vs. 'difficult'. Birth weight and almost all calf dimensions were significantly related to ease of calving. All simple relationships involving dam traits lacked significance in H and DF heifers, except precalving hip width in the latter group. DRW heifers experiencing difficult calving were on average heavier and larger framed. Excluding calf dimensions, birth weight was the first variable to enter into the discriminant functions in all three breed groups. Dam traits contributing to discrimination between calving performance categories were depth of chest in H heifers, heart girth, chest width and pinbone distance in DRW heifers, and pelvic height in DF heifers. The possible significance of these effects is discussed.

Key words: Dystocia, discriminant analysis, dam traits, dairy cattle

[Aspects morphologiques de la dystocie chez les génisses laitières et à deux fins.]
Titre abrégé: Aspects morphologiques de la dystocie.
Nous avons étudié les rapports phénotypiques entre la facilité de vêlage et un certain nombre de caractéristiques des mères (surtout morphologiques) au moyen de l'analyse discriminatoire pas à pas. Nous avons noté à cette fin le poids, les mensurations et les mesures du gras de couverture et de la teneur en chair de 79 génisses Holstein (H), 90 Rouges et Blanches hollandaises (DRW) et 104 Frisonnes hollandaises (DF) dix jours après la mise bas. Les mensurations notées étaient les suivantes: longueur du corps, hauteur aux hanches et au garrot, largeur et profondeur de poitrine, périmètre thoracique, largeur aux hanches et mesure du "tour spiral". Pour la moitié des génisses environ, nous disposions de données sur les dimensions du pelvis avant la mise bas: hauteur et largeur de l'ouverture pelvienne, largeur aux hanches et à l'articulation de la cuisse, distance entre les pointes de fesse, distances horizontales et verticales entre la hanche et l'articulation de la cuisse et entre la hanche et la pointe de fesse. Le poids à la naissance de tous les veaux et les mensurations des veaux vivants avaient aussi été notés. Le vêlage était qualifié de "facile" (peu ou

pas d'aide), "normal" (traction facile) ou "difficile' (traction difficile ou césarienne). En outre, nous avons mesuré la force exercée par une vêleuse pour un certain nombre de mises bas de chacune de ces catégories. L'analyse de ces données sur la traction exercée a montré que la différence entre une mise bas "facile" et une mise bas "normale" tenait plus à des facteurs subjectifs et à la chance que la différence entre une mise bas "normale" et une mise bas "difficile". Par ailleurs, il y avait un rapport significatif entre la facilité de vêlage d'une part, et le poids à la naissance et la plupart des mensurations des veaux d'autre part. Aucun des rapports simples étudiés et incorporant des caractéristiques des mères n'était significatif dans le cas des génisses H et DF, à l'exception de la largeur des hanches avant la mise bas chez les DF. Les génisses DRW éprouvant des difficultés à vêler étaient en moyenne plus lourdes et plus grosses. Exception faite des mensurations des veaux, le poids à la naissance était la première variable à faire partie des fonctions discriminatoires chez les trois races. Les caractéristiques des mères contribuant à la discrimination entre les catégories de facilité de vêlage étaient la profondeur de poitrine chez les génisses H, le périmètre thoracique, la largeur de poitrine et la distance entre les pointes de fesse chez les génisses DRW, et la hauteur de l'ouverture pelvienne chez les génisses DF. Nous discutons de la signification possible de ces effets.

Mots clés: Dystocie, analyse discriminatoire, caractéristiques des mères, bovins laitiers

Dystocia is a major cause of stillbirth and early calf mortality, and consequently of considerable economic importance. Incidences encountered in first calf heifers are three to four times higher than in cows (Pollak and Freeman 1976; Gaillard 1980). Most of the current breeding strategies in dairy and dual purpose cattle aim for a short-term reduction of problems in the former age group, by identifying low-risk bulls for mating to maiden heifers (Philipsson et al. 1979). Though selective use of bulls will reduce calving problems in heifers rapidly (Bar-Anan 1979; Philipsson 1979), there will hardly be any genetic change when the high-risk bulls are used on cows (Philipsson et al. 1979). In beef and dual purpose cattle, actual selection of sires of calf to reduce dystocia may not even be very appealing, as it will almost inevitably entail a reduction in birth weight, considering the high genetic correlation between these traits ($r_g \simeq 0.9$; Philipsson 1976a; Pollak and Freeman 1976; Gaillard 1980). The alternative, selection of sires for daughter calving performance, seems to have more potentials in this case, as the estimates for the genetic correlation between birth weight and dystocia as dam traits are lower ($r_g \simeq 0.65$; Philipsson et al. 1979; Gaillard 1980; Burfening et al. 1981). The correlated response in such a selection program could be controlled by the use of an index with restriction on birth weight. Alternatively, it might be feasible to select for traits contributing to maternal calving performance. In this field, attention has focussed on pelvic inlet dimensions. The size of the pelvic inlet proved to be associated with probability of dystocia (e.g. Rice and Wiltbank 1972; Menissier 1975a,b), though it accounted for at most 10% of the variance in dystocia rate. However, pelvic inlet dimensions are difficult to measure which limits their use in a progeny testing program. Simply measurable dam traits like body weight and body dimensions (body length, heart girth, hip weight, etc.) are, on the other hand, only weakly associated with calving ease (e.g. Hansen 1975; Hässig and Schlote 1980). Data on the relationship between ease of calving and more specific indicators of shape and position of the rump are scarce. Work by Philipsson (1976b) suggests that maternal calving performance may be favorably associated, at least in the genetic sense, with low placed thurls and pinbones, i.e. a roof-shaped rump.

In the present paper we have attempted to identify morphologic dam traits with significant phenotypic effects on calving performance of dairy and dual purpose heifers in addition to birth weight, using discriminant analysis.

MATERIALS AND METHODS

Animals and Measurements

During a 4-yr period (1978–1982), data were collected on all parturient heifers and on their progeny, at the 'Gen' experimental station at Lelystad. The dairy herd, consisting of about 250 purebred Holstein, Dutch Red and White and Dutch Friesian lactating heifers and cows, had been involved in a breed comparison study since 1972. Purebreeding was maintained during the period of data collection. The heifers were bred by AI (10 different bulls per breed per year) to calve at 2 yr of age. A body weight of 300–325 kg at breeding was pursued. The herd was kept indoors from November to April and pregnant heifers were fed a mixture of grass silage (75%) and corn silage (25%), supplemented with 1 kg of concentrates during the last two weeks of gestation. Otherwise the herd was kept outdoors on high quality pasture.

A number of internal and external pelvic dimensions were measured 3 wk before the expected calving date (Table 2; Fig. 1). Height (the perpendicular distance between the cranial end of the symphisis pubis and the ventral surface of the midsacrum) and width (maximum distance between the shafts of the ilia) of the pelvic inlet were measured rectally by a sliding calliper (Ben David 1960) after epidural anesthesia. Horizontal and vertical distances between hip and thurl and hip and pinbone (Philipsson 1976b) were measured with a pair of perpendicularly linked marking gauges fitted with a spirit level. Distances between pinbones and width at hips and thurls were measured additionally. Data on pelvic inlet dimensions and horizontal and vertical distances were collected only in the first 2 yr of the study. All measurements were made in duplicate and the averages were used in the analysis.

Newborn calves were weighed at birth. Measurements were made in live calves within 96 h after birth, as detailed in Table 1. Heifers were weighed and measured about 10 days after calving, as detailed in Table 3. Fat covering and muscularity were scored visually on an 18-point scale.

Calving was supervised and assisted as necessary. Calving performance was scored as 'easy' (no or minor assistance), 'normal' (easy pull), or 'difficult' (hard pull or Caesarean). In an attempt to judge calving ease more objectively, forces exerted on the calf by calf puller were measured at 113 calvings (heifers as well as cows). This was achieved by attaching the ropes of the calf puller to force recording devices connected to a graphic recorder.

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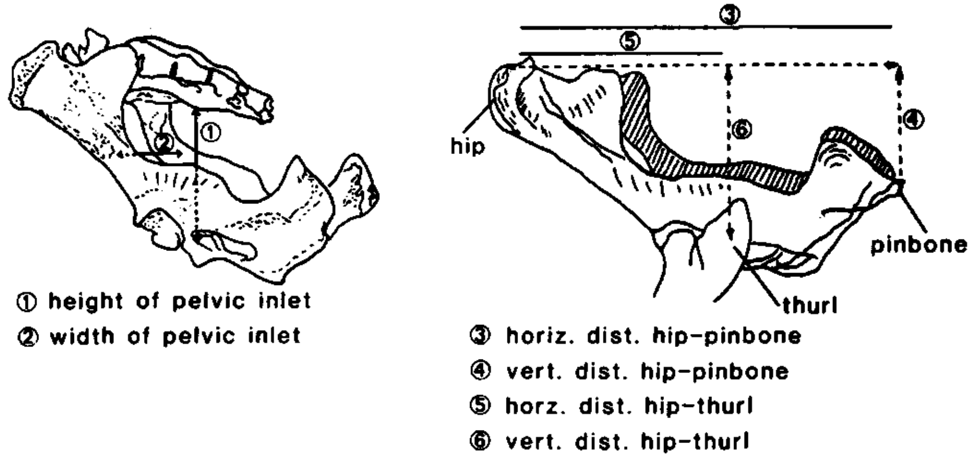

Fig. 1. Pelvic dimensions recorded on heifers prior to calving.

Table 1. Average birth weights and dimensions† (± SD) of purebred Holstein (H), Dutch Red and White (DRW) and Dutch Friesian (DF) calves from heifers, by calving performance score

		Score			
	Breed	Easy	Normal	Difficult	Sign
Number‡	H	22	35	10	
	DRW	19	47	9	
	DF	25	63	4	
Birth weight (kg)	H	37.2 ± 3.5	41.1 ± 4.7	44.8 ± 3.9	***
	DRW	32.7 ± 5.8	36.4 ± 3.5	41.9 ± 6.1	***
	DF	32.1 ± 3.8	34.8 ± 3.4	37.0 ± 3.0	***
Body length (cm)	H	67.5 ± 2.4	69.6 ± 3.3	71.6 ± 3.8	**
	DRW	62.4 ± 3.7	64.0 ± 2.8	66.6 ± 3.8	***
	DF	62.9 ± 3.1	64.9 ± 2.9	66.8 ± 2.8	**
Height at withers (cm)	H	73.4 ± 2.6	76.2 ± 2.0	77.7 ± 2.9	***
	DRW	67.4 ± 3.7	69.8 ± 1.9	72.8 ± 3.3	***
	DF	71.0 ± 2.3	71.1 ± 2.5	73.0 ± 2.6	NS
Height at hips (cm)	H	75.6 ± 3.3	78.4 ± 2.7	80.1 ± 2.4	***
	DRW	69.8 ± 4.2	72.5 ± 2.2	75.6 ± 2.6	***
	DF	73.0 ± 2.0	73.2 ± 2.5	76.3 ± 0.6	*
Chest width (cm)	H	15.2 ± 0.9	15.3 ± 1.1	15.6 ± 0.6	NS
	DRW	14.8 ± 1.5	15.6 ± 1.9	16.3 ± 1.4	**
	DF	14.6 ± 0.9	15.2 ± 0.9	15.5 ± 1.3	*
Shoulder width (cm)	H	19.5 ± 1.1	19.6 ± 1.4	20.5 ± 0.9	NS
	DRW	18.4 ± 2.6	19.9 ± 1.3	20.6 ± 1.5	**
	DF	18.1 ± 1.4	19.0 ± 1.1	19.3 ± 0.9	**
Chest depth (cm)	H	27.1 ± 1.8	28.2 ± 1.5	30.1 ± 1.8	***
	DRW	25.0 ± 1.9	26.2 ± 1.6	26.4 ± 2.2	*
	DF	26.0 ± 1.6	26.2 ± 1.4	27.9 ± 2.3	NS
Hip width (cm)	H	15.8 ± 1.0	16.3 ± 1.0	17.2 ± 1.0	**
	DRW	15.5 ± 1.8	16.1 ± 1.0	16.9 ± 1.6	*
	DF	15.5 ± 1.3	15.7 ± 0.9	16.8 ± 1.0	NS
Thurl width (cm)	H	20.9 ± 0.9	21.4 ± 1.1	22.3 ± 0.8	**
	DRW	19.6 ± 1.9	20.9 ± 1.1	21.8 ± 1.8	***
	DF	20.4 ± 1.5	20.5 ± 0.9	22.0 ± 1.8	*
Cannonbone diam. (cm)	H	2.88 ± 0.29	2.99 ± 0.23	3.10 ± 0.24	NS
	DRW	2.92 ± 0.21	3.10 ± 0.20	3.35 ± 0.15	***
	DF	2.82 ± 0.26	2.89 ± 0.23	3.03 ± 0.26	NS

†Calves alive at time of measurement.

‡Relates to calf dimensions; number of observations on birth weight are 26, 29, 14 (H); 20, 54, 16 (DRW); 26, 69, 8 (DF).

*,**,*** = $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively, by F = MS between groups/MS within. NS, $P > 0.05$.

presentations and gestation periods outside the range of 261–290 days, data from 79 Holstein, 90 Dutch Red and White and 104 Dutch Friesian heifers were available for analysis.

Statistical Analysis

Although a stepwise multiple regression procedure might be considered appropriate for the problem addressed here, the subjectivity involved in assigning weights to the categories of calving performance presents a major problem. Simply by rescaling, an intrinsic linear relationship may become non-linear and vice versa. Other problems originating from the categorical nature of the response variable are non-normality and heterogeneity of error variance. Thus, conditions for correct statistical inferences within the analysis of variance framework are not met. More appropriate techniques in this case are logistic regression and discriminant analysis (Fienberg 1981). The data were analyzed by stepwise linear discriminant analysis, using the SPSS-version (Klecka 1975). In this procedure observations in each calving performance category are considered as a separate group, whereas the discriminating variables are assumed multivariate normally distributed within each group, with equal covariance matrices. The procedure is supposed to be rather insensitive to deviations from these assumptions, however (Klecka 1975). A brief outline of the procedure used is presented in the Appendix.

The data for the different breeds were analyzed separately because phenotypic differences in the relationship between calving ease and the traits studied were anticipated.

RESULTS

Figure 2 presents a typical example of the force patterns recorded at deliveries judged as 'normal'. Its highly irregular shape is caused by the straining bouts of the cow and by pulling alternately on the left and right leg of the calf. The pattern depends on a number of factors, e.g. the stage of calving at which pulling is started, pulling behavior, intensity of labor and the degree of friction between the calf and the birth canal. Although an attempt was made to standardize the calving procedure by delaying pulling on the calf until the nostrils were visible and to pull only during a straining bout, complete elimination of human influence is of course not possible. From the options available to characterize the force patterns, the maximum force was chosen. The association between the maximum force recorded and independently judged calving ease is shown in Fig. 3. The maxima recorded varied from about 75 to 325 kg, averaging 131 ± 44 kg for deliveries judged as easy, 158 ± 45 kg for normal, and 262 ± 45 kg for difficult calvings. Although the pairwise differences in average maximal force between the calving performance categories were significant ($P<0.05$), a

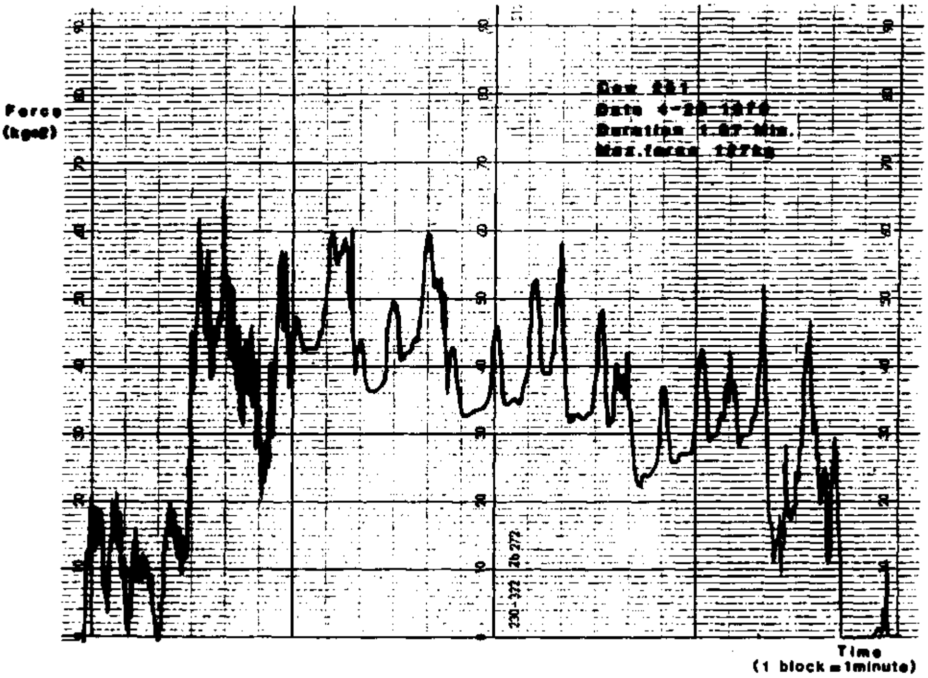

Fig. 2. A typical example of the force patterns recorded on calf puller ropes during delivery.

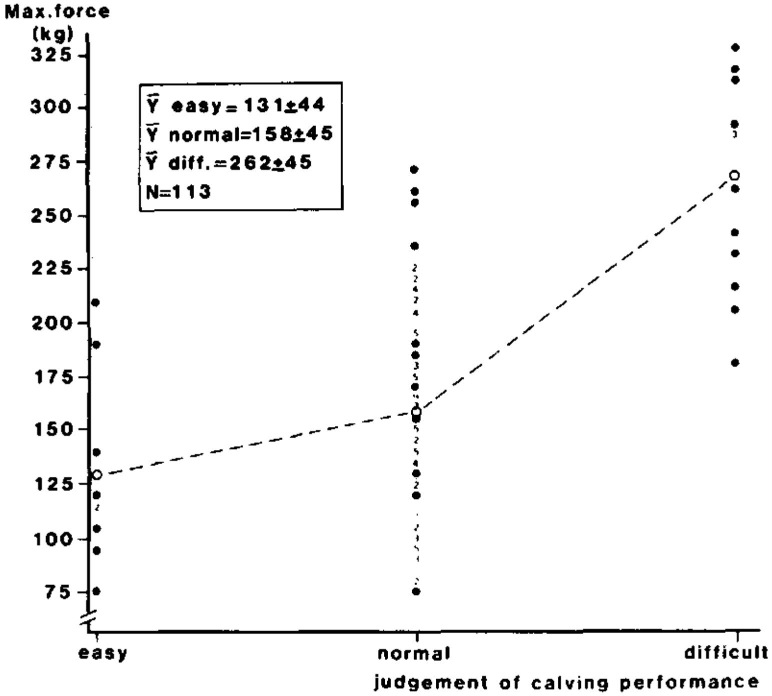

Fig. 3. Maximum forces recorded at deliveries judged as easy, normal and difficult (numbers indicate number of coinciding observations).

considerable overlap can be observed, particularly between deliveries classified as 'easy' and 'normal'.

The average values of the traits measured within the calving performance categories are summarized in Tables 1 to 3. The data in Table 1 confirm the well-established association between ease of calving and calf weight or size; a higher degree of difficulty was associated with a significant increase in birth weight and in most of the measurements recorded. The average dimensions of the pelvic inlet area did not differ significantly ($P>0.05$) between calving performance categories for any of the breed groups (Table 2), although heifers having difficult calvings tended to have less pelvic inlet height. The horizontal and vertical rump dimensions, measured to characterize the shape and position of the rump, did not appear to be related to calving ease. Precalving width at hips and thurls was negatively associated with calving ease in Dutch Friesian and Dutch Red and White heifers, respectively. There was no significant simple relationship between postcalving body weight, body dimensions, fat covering and muscularity, and calving ease in Holstein and Dutch Friesian heifers (Table 3). However, the Dutch Red and White heifers with a higher degree of calving difficulty were on average significantly heavier and larger framed, as indicated by height and width at hips, heart girth and spiral girth.

The results of the discriminant analyses are presented in Table 4. Calf measurements were excluded because dead calves had not been measured. In the Holstein group, weight of calf and chest depth of dam contributed, in this order, significantly to discrimination between calving performance categories, as indicated by the values of Wilks' lambda, a statistic for overall discrimination between groups (see Appen-

Table 2. Average pelvic inlet and external rump dimensions (± SD) in Holstein (H), Dutch Red and White (DRW) and Dutch Friesian (DF) heifers, by calving performance score

		Score			
	Breed	Easy	Normal	Difficult	Sign
Number†	H	11–26	20–38	8–13	
	DRW	15–20	42–51	14–16	
	DF	13–24	49–68	5–8	
Height of inlet (cm)	H	17.7±0.7	17.5±1.2	17.4±1.5	NS
	DRW	17.0±0.8	17.2±0.7	17.5±0.8	NS
	DF	16.5±1.1	16.1±0.9	15.8±0.8	NS
Width of inlet (cm)	H	15.6±1.1	15.7±1.4	15.8±1.2	NS
	DRW	14.4±0.9	14.9±0.9	14.9±0.9	NS
	DF	14.9±1.4	15.0±1.0	14.9±1.2	NS
Hip-pinbone (horiz.)(cm)	H	47.6±1.9	46.9±2.5	46.8±1.6	NS
	DRW	43.7±1.6	44.0±1.7	44.4±2.6	NS
	DF	43.7±1.9	43.8±1.7	43.9±1.8	NS
Hip-pinbone (vert.)(cm)‡	H	–	–	–	
	DRW	8.4±2.8	9.3±2.5	9.2±1.8	NS
	DF	-	–	–	
Hip-thurl (horiz.)(cm)	H	27.3±3.1	26.6±2.2	27.2±1.5	NS
	DRW	26.0±2.2	25.2±1.9	25.7±3.0	NS
	DF	25.3±2.5	25.1±2.3	24.8±1.0	NS
Hip-thurl (vert.)(cm)	H	16.5±1.9	17.8±2.2	16.5±2.6	NS
	DRW	16.5±2.4	16.3±2.3	17.2±2.1	NS
	DF	15.3±2.3	16.1±2.0	15.2±1.5	NS
Hip width (cm)	H	50.9±2.1	51.4±2.8	51.7±2.4	NS
	DRW	51.1±2.2	52.1±1.9	52.3±3.0	NS
	DF	51.8±2.7	53.4±2.3	54.4±1.7	**
Thurl width (cm)	H	48.2±1.8	48.6±2.3	48.6±1.9	NS
	DRW	48.3±2.3	48.8±1.8	50.0±2.2	*
	DF	48.7±2.0	49.3±1.7	49.5±1.7	NS
Pinbone distance (cm)	H	18.1±1.4	18.2±1.2	18.4±1.3	NS
	DRW	18.5±1.2	17.7±1.4	17.7±1.7	NS
	DF	19.1±1.7	18.8±1.4	19.3±1.3	NS

†Lowest numbers for distances between hip and pinbone; highest numbers for hip width, thurl width and pinbone distance.

‡Not measurable in a number of H and DF heifers due to rump shape; means would therefore be biased.

*,**$P \leq 0.05$ and $P \leq 0.01$ respectively, by F = MS between groups/MS within. NS, $P > 0.05$.

dix). The F-statistics for pairs of groups indicated that these two variables accomplished a significant difference between easy vs. normal, and normal vs. difficult calvings. The relative contribution of the first eigenvalue was 94.8%, indicating that discrimination was predominantly in one of the two orthogonal directions possible as might be expected for an ordered classification. One discriminant function was therefore considered sufficient. The normalized coefficient for birth weight was about twice the coefficient for chest depth of the dam and opposite in sign. This suggests that for a given calf weight, ease of calving was favored by an increase in chest development of the dam.

In the Dutch Red and White group, birth weight entered as first discriminating variable as well. In addition, heart girth, chest width and pinbone distance of dam contributed significantly. The discrimination ob-

Table 3. Average body weights, body dimensions, and scores for fat covering and muscularity (± SD) in Holstein (H), Dutch Red and Whilte (DRW) and Dutch Friesian (DF) heifers, by calving performance score

		Score			
	Breed	Easy	Normal	Difficult	Sign.[1]
Number	H	26	38	13	
	DRW	20	53	16	
	DF	25	70	7	
Body weight (kg)	H	484.9±44.9	494.6±39.0	468.0±43.8	NS
	DRW	464.3±40.1	487.2±45.8	511.8±56.7	*
	DF	458.6±33.5	464.6±37.2	476.4±59.4	NS
Body length (cm)	H	151.5± 6.2	152.9± 5.2	152.1± 7.6	NS
	DRW	144.2± 5.0	145.3± 6.6	147.2± 6.4	NS
	DF	143.2± 3.6	145.1± 5.2	143.7± 4.1	NS
Height at withers (cm)	H	131.7± 3.5	131.9± 4.0	131.5± 4.9	NS
	DRW	121.2± 3.9	119.9± 2.6	121.7± 4.1	NS
	DF	124.4± 3.2	124.5± 3.6	124.4± 3.0	NS
Height at hips (cm)	H	135.3± 3.4	135.7± 4.2	135.5± 4.9	NS
	DRW	125.6± 2.5	125.6± 2.7	128.4± 3.8	**
	DF	127.5± 3.3	128.1± 2.9	127.9± 4.5	NS
Chest width (cm)	H	43.2± 4.0	42.4± 4.4	41.2± 4.5	NS
	DRW	43.9± 3.3	45.9± 3.9	46.3± 3.5	NS
	DF	45.0± 3.7	44.8± 3.6	44.3± 3.5	NS
Chest depth (cm)	H	70.8± 2.1	71.1± 3.1	69.7± 3.2	NS
	DRW	65.7± 2.7	66.9± 2.2	68.5± 3.2	**
	DF	68.0± 2.2	68.3± 2.3	68.6± 2.3	NS
Heart girth (cm)	H	187.8± 8.1	187.6± 7.1	185.4± 7.7	NS
	DRW	179.9± 6.0	184.0± 7.3	188.9± 8.5	**
	DF	184.8± 6.3	185.8± 6.3	186.4± 7.1	NS
Spiral girth (cm)	H	236.3± 8.8	237.1± 8.7	233.5± 8.2	NS
	DRW	228.4± 6.5	231.3± 7.6	234.7± 8.2	*
	DF	230.5± 7.4	230.1± 6.8	231.7± 7.3	NS
Hip width (cm)	H	50.2± 2.9	50.2± 2.4	50.1± 2.2	NS
	DRW	49.9± 2.2	51.0± 2.3	51.9± 2.5	*
	DF	50.9± 2.3	52.3± 2.8	51.9± 3.1	NS
Fat covering (1–18)	H	5.1± 1.8	4.9± 1.9	3.7± 1.4	NS
	DRW	6.5± 1.5	7.1± 1.0	6.6± 1.5	NS
	DF	6.8± 0.9	6.8± 1.3	6.7± 1.3	NS
Muscularity (1–18)	H	3.9± 1.2	3.8± 1.5	3.5± 1.9	NS
	DRW	7.0± 0.8	7.1± 0.7	7.1± 1.3	NS
	DF	6.9± 0.7	6.9± 1.5	7.3± 1.3	NS

[1] *,**$P \leq 0.05$ and $P \leq 0.01$, respectively by F = MS between groups/MS within. NS, $P > 0.05$.

tained by these four variables was very significant ($\Lambda = 0.38$). All three calving performance categories were clearly distinguished, again predominantly in one direction. The coefficients of the only discriminant function of importance showed that calving performance was adversely affected by increases in weight of the calf or heart girth of dam, and favored by increases in chest width or pinbone distance, given the remaining three variables.

In the Dutch Friesian group height of pelvic inlet contributed significantly to the discrimination between calving performance categories, in addition to birth weight. The discrimination accomplished by these two variables was rather low, however, with no significant discrimination between normal

Table 4. Results of stepwise discriminant analysis on calving performance categories in Holstein (H), Dutch Red and White (DRW) and Dutch Friesian (DF) heifers

Breed	Variables entered consecutively	Λ†	Fe-n‡	Fn-d§	λ_1¶	d//
H	1. Birth weight	0.71**				1.113
	2. Chest depth	0.63**	7.73***	5.70**	94.8%	−0.557
DRW	1. Birth weight	0.61**				0.846
	2. Heart girth	0.52**				1.136
	3. Chest width	0.46**				−0.671
	4. Pinbone distance	0.38**	9.05***	8.99***	97.1%	−0.589
DF	1. Birth weight	0.88*				0.876
	2. Pelvic inlet height	0.76**	9.12***	0.55N.S.	99.8%	−0.774

†Wilks lambda (cumulative), ranging from 1 (no discrimination) to 0 (complete discrimination).

‡*F*-statistic for distance easy-normal after inclusion of last significant variable.

§*F*-statistic for distance normal-difficult after inclusion of last significant variable.

¶Relative eigenvalue of first discriminant function.

//Normalized coefficients of first discriminant function.

*,**,***$P<0.05$, $P<0.01$ and $P<0.001$, respectively; NS, $P>0.05$.

and difficult calvings. The latter was most probably a result of the small number of difficult deliveries in this breed group. The signs of the coefficients of the only discriminant function of importance indicated a favorable effect on calving ease by an increase in pelvic height and an unfavorable effect by an increase in birth weight, as might have been anticipated.

DISCUSSION

The recording of the forces exerted on the calf during delivery was induced by dissatisfaction about the subjectivity involved in classifying calving ease. The force curves are also subject to some variability in human judgement because the delivery procedure cannot be standardized completely. However, their degree of objectivity is expected to be higher than the subjective classification. Consequently they may serve as a check on the classification procedure. The characterization of the force curves by their maximum does not imply that the maximum has more significance than other parameters, e.g. total force exerted or time required for delivery. All three parameters were in fact highly correlated ($r = 0.75$). The maximum forces exerted on the calf during delivery indicate that more subjectivity or chance was associated with classifying easy vs. normal than normal vs. difficult deliveries. Thus, equidistant scoring might not have been justified.

The association between weight and dimensions of newborn calves, and calving ease, has been demonstrated previously for the Charolais (Menissier 1975b) and Simmental (Hässig and Schlote 1980) breeds. In the detailed study by Hässig and Schlote (1980) there was no association between calf dimensions and ease of calving if birth weight was controlled. Thus, in that study birth weight was a good indicator of calf size, which is in agreement with the high correlations ($r = 0.7–0.9$) between birth weight and most calf dimensions in Dutch Friesian and Dutch Red and White male calves (Van der Meij 1973). The importance of birth weight, or calf size, for ease of calving is underlined by the fact that it entered as the first variable into the discriminant functions in every breed group.

In the present study, there was no significant relationship between calving ease and pelvic inlet dimensions in Holstein and Dutch Red and White heifers. These results are not in accord with previous observations in Angus, Hereford and Charolais heifers (Rice and Wiltbank 1972; Menissier 1975a,b; Price and Wiltbank 1978). However, an increase in the height of the pelvic inlet appeared to favor calving ease of Dutch Friesian heifers (Table 2). It is interesting to note that the Dutch Friesians have been selected for a flat rump.

The suggestion by Philipsson (1976b) that calving performance is favored by a 'roof-shaped' rump was not confirmed in the present study. However, in a number of instances the horizontal and vertical rump dimensions were difficult to measure. Relatively large errors are to be anticipated in taking these measurements (Meijering et al. 1978). Such errors could have influenced the results. Besides, the phenotypic association was examined in the present study whereas Philipsson (1976b) discussed the genetic relationship.

Previous studies (Rice and Wiltbank 1972; Hansen 1975; Menissier 1975b; Hässig and Schlote 1980) have established that body weight and external body dimensions of the primiparous dam are not closely related to ease of calving. In the present study the average body dimensions of Holstein heifers in different calving performance categories did not differ significantly (Table 3). Heifers calving with difficulty tended to have less body development, however, as indicated by weight, chest depth, heart girth and spiral girth. In the multivariate analysis an increase in chest depth of Holstein heifers contributed favorably to ease of calving. These results indicate that a number of the Holstein heifers probably lacked sufficient body development at calving and should have been bred at a later age. In the Dutch Red and White group, the results are somewhat puzzling. The average body dimensions (Table 3) indicated that larger framed heifers were more likely to calve with difficulty. Menissier (1975b) suggested that the positive relationship between dam and calf size (Bellows et al. 1971; Laster 1974) might cause an unfavorable ratio between calf size and pelvic inlet dimensions, particularly in breeds with heavier muscling. However, in the present study the correlation between calf size and heart girth was only 0.3, and after conditioning for birth weight in the discriminant analysis the chest dimensions still contributed significantly, whereas the pelvic inlet dimensions did not. As heart girth and chest width appeared in the discriminant function with opposite sign, the influence of chest development on calving ease in this group remains unclear.

The extent of fat covering and the degree of muscularity had no influence on calving ease, which is consistent with results of other studies (Bellows et al. 1971; Hässig and Schlote 1980).

The data base of this study is limited in its volume. Caution is therefore advised when looking at the results and drawing conclusions. However, it can be concluded that size of calf is most important for calving ease within each of the breed groups. There are some indications which, of the dam dimensions, may influence calving ease. However, none of these appears to exert a strong and consistent influence. It should be noted that these results do not exclude the existence of significant genetic relationships between ease of calving and dam dimensions. For, in the absence of environmental covariance, the phenotypic correlation equals the product of the genetic correlation and the square root of the heritabilities. Taking $h^2 = 0.1$ for calving ease (Philipsson et al. 1979) and $h^2 = 0.4$ for a dam dimension, the genetic correlation is expected to be five times as high as the phenotypic correlation.

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APPENDIX

Brief Outline of the Stepwise Discriminant Analysis Procedure Applied.

Significant discriminatory variables are selected by performing the following sequence:

1. A likelihood ratio test (under normality) for equality over groups of the conditional distribution of each variable already entered into the set of discriminatory variables, given all other variables entered.
2. Elimination of the least useful of the variables with not significantly different conditional distributions over groups.
3. A similar likelihood ratio test for each variable not yet entered, given the variables entered.
4. Inclusion of one significant variable, according to a predetermined criterion.

This sequence is repeated until none of the potentially discriminatory variables meets the significance threshold for elimination or inclusion. Let, for example, X_1 to X_4 be the discriminatory variables considered, and let X_1 and X_2 be included in previous steps. Now $f(X_1|X_2)$ and $g(X_2|X_1)$ are tested. If e.g. $f(X_1|X_2)$ is not significant, X_1 is removed and $h(X_3|X_2)$ and $j(X_4|X_2)$ are tested. If neither of these is significant, the stepwise procedure is terminated and X_2 will be the only variable in the discriminant function. However, if, for example, $h(X_3|X_2)$ is significant, X_3 is included, or if both $h(X_3|X_2)$ and $j(X_4|X_2$ are significant, either X_3 or X_4 is included, depending on which variable accomodates best to the predetermined criterion. In both situations the stepwise procedure continues. In the present study the significance threshold for elimination and inclusion was set at 5%. The variable maximizing the lowest value of the F-statistic for the multivariate difference between a pair of group means (MAXMINF) was selected for inclusion at each consecutive step. A summary of the test statistics can be found in the BMD-manual (Biomedical Computer Programs 1973).

The last significant variable having been entered, the coefficients of the discriminant functions are computed. Let $z_i = \mathbf{d}_i\,\mathbf{x}$ be the ith discriminant function (in the case of three groups $i \leq 2$), where $\mathbf{d}_i$ is the vector of unknown coefficients for the set of significant variables $\mathbf{x}$ scaled by their respective standard deviations. The coefficient vectors $\mathbf{d}_i$ are constructed from the eigenvectors of the matrix $\mathbf{BW}^{-1}$, the product of the between group (**B**) and the inverted within group (**W**) crossproduct matrices. The corresponding eigenvalues may give an indication of the relative importance of the discriminant functions in the discrimination. When one eigenvalue dominates the others, the group means are nearly collinear, and the first discriminant function may be sufficient for discrimination in practice. The coefficients of the standardized variables in the ith function are proportional with respect to their contribution in discrimination.

The equality of multivariate group means at each step may be tested by Wilks' lambda ($\Lambda = |\mathbf{W}|/|\mathbf{B} + \mathbf{W}|$, with degrees of freedom p, g-1, n-g) or its associated chi-square-statistic ($\chi^2 = -n \ln \Lambda$ with $p(g\text{-}1)$ degrees of freedom), where:

p = number of variables entered
g = number of groups
n = total number of observations

Λ ranges from 1 (no discrimination) to 0 (maximal discrimination).

Chapter 6

Responses to sire selection for dystocia

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RESPONSES TO SIRE SELECTION FOR DYSTOCIA

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ABSTRACT

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The hypothesis that low-risk bulls for dystocia sire small calves, which develop into small heifers and which calve with more difficulty was tested in a two-way sire-selection trial with Holstein (HF), Dutch Red and White (DRW) and Dutch Friesian (DF) cattle in pure breeding. Low-risk (L) and high-risk (H) bulls were selected from sire summaries to sire F_1 calves. Birth traits (ease of birth, gestation length, weight and dimensions) of F_1 calves, and body development of F_1 females, were monitored. Within sire groups, F_1 females were in turn bred to low-risk (L^*) and high-risk (H^*) sires. Birth traits of F_2 calves were recorded. Quantitative and categorical traits were analysed by ordinary least-squares and generalized linear model procedures, respectively.

Differences between sire groups for ease of birth and gestation length of F_1 calves were significant ($P < 0.10$) in the DRW breed only; for calf weight and dimensions, there was no such breed-by-sire group interaction. F_1 females sired by L and H bulls showed only minor differences in body development during rearing and after first calving. Effects of both maternal grandsire group (L against H) and sire group (L^* against H^*) were significant for birth traits of F_2 calves, and additive. Maternal grandsire group effect on ease of birth was not significant in the DF breed, however. In the DRW breed, the equality of signs of sire group contrast in F_1 and maternal grandsire group contrast in F_2 calves supports the conclusion from studies on field data that direct and maternal grandsire genetic merits for ease of birth are correlated positively. This conclusion was neither supported nor contradicted by the results from the Black and White breeds. The results indicate that the hypothesis stated above has to be rejected, and it is conjectured that the maternal grandsire effect on ease of birth is dominated by direct inheritance of calf size.

INTRODUCTION

In order to reduce the incidence of dystocia, most of the current sire-evaluation schemes include some programme to identify low-risk bulls for heifer matings (Philipsson et al., 1979). A consistent use of such bulls yields a rapid short-term reduction in problems at first calving (Bar Anan, 1979; Philipsson, 1979). In The Netherlands however, herdsmen are often reluctant to use the low-risk bulls available. A common hypothesis is that these bulls sire small calves resulting in small heifers that run an increased risk of dystocia. In view of the size and sign of the genetic correlation between dystocia and birth weight ($r_g \cong 0.9$; Meijering, 1984), the probability of low-

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risk bulls siring small calves is indeed high. The second part of the hypothesis was examined by Thompson and Rege (1984) but has not yet been proved. It is probably rather an incorrect interpretation of the negative correlation between direct and maternal genetic components ($-0.63 < r_{DM} < -0.16$; Philipsson, 1976; Gaillard, 1980; Thompson et al., 1981; Dwyer and Schaeffer, 1984). In predicting the genetic merit for daughters' calving ease of bulls with "known" direct genetic merit, it is not this correlation, but the regression of maternal grandsire merit on direct genetic merit that is relevant. In terms of direct (σ_D^2) and maternal (σ_M^2) components of variance and direct-maternal genetic covariance (σ_{DM}), following Koch (1972) and Willham (1972), the regression coefficient equals $b_{mgs,s} = (\frac{1}{8}\,\sigma_D^2 + \frac{1}{4}\,\sigma_{DM})/\frac{1}{4}\,\sigma_D^2 = \frac{1}{2} + r_{DM}\,(\sigma_M/\sigma_D)$. The expected response in daughter dystocia is obviously then only antagonistic to the expected direct response if $r_{DM} < -\sigma_D/2\sigma_M$. Estimates for σ_D/σ_M from the data given by Thompson et al. (1981) ($r_{DM} = -0.38$) and Dwyer and Schaeffer (1984) ($r_{DM} = -0.27$) are 1.11 and 0.97, respectively. In both cases $r_{DM} > -\sigma_D/2\sigma_M$ and $0 < b_{mgs,s} < 0.25$. These studies indicate that the regression of maternal grandsire merit on direct genetic merit may be positive, though close to zero.

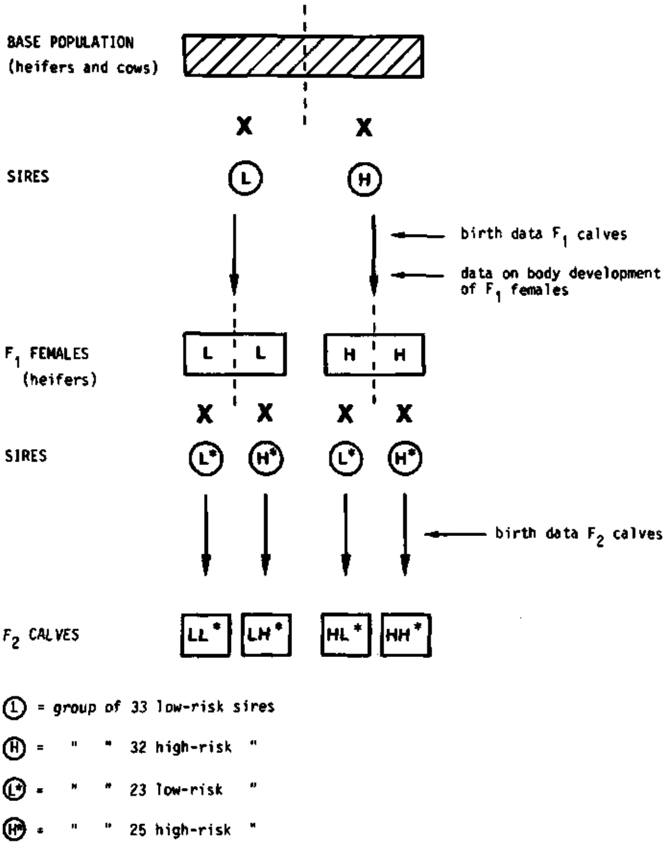
We examined the hypothesis that low-risk bulls sire small calves which develop into small heifers and which have more difficulty at calving, in a two-way sire-selection trial.

MATERIALS AND METHODS

Animals and design

The trial was conducted at the "Gen" Experimental Station at Lelystad from 1978 until 1983. The dairy herd, consisting of about 250 pure-bred (lactating) Holstein (HF), Dutch Red and White (DRW) and Dutch Friesian (DF) cows, had been involved in a breed-evaluation study since 1972 (Oldenbroek, 1974). Pure breeding was maintained throughout the trial. Details on herd management are given elsewhere (Meijering and Postma, 1984).

A schematic representation of the trial is given in Fig. 1. Maiden heifers in 1978 and 1979, and lactating cows from 1978 till 1980 were assigned randomly to proven bulls presenting either a low (L sires) or a high (H sires) risk of dystocia according to Dutch and United States sire summaries. A total of 33 L sires (14 HF, 10 DRW, 9 DF) and 32 H sires (11 HF, 9 DRW, 12 DF) were used over these years. Calving was supervised and assisted as necessary. Calving was scored as 'easy' (no or minor assistance), 'normal' (easy pull) or 'difficult' (hard pull or Caesarean). Additional birth traits recorded were birthweight, gestation length and calf sizes (live calves only). After omitting incomplete records, twin births, abnormal presentations and gestation periods outside the range of 261—290 days, data from 682 calves of the F_1 generation were available for analysis.



Note: Holsteins, Dutch Red and Whites and Dutch Friesians in pure breeding.

Fig. 1. Design of the trial.

As many female F_1 calves as possible were kept in the herd. They were reared with free access to roughage and mated at 14—15 months of age. During rearing, body weights and sizes were established at three-monthly intervals. At mating the F_1 females within each sire line (L or H) were randomly assigned to low-risk (L* sires) or high-risk (H* sires) bulls. A total of 23 L* sires (6 HF, 9 DRW, 8 DF) and 25 H* sires (8 HF, 9 DRW, 9 DF) were used to sire the F_2 generation. Some of these had also been used to sire the F_1 generation. Traits recorded at birth of F_2 calves were ease of birth (scored as outlined), birthweight and gestation length. Dams were weighed and measured 10 days after calving. After omitting exceptional data, records from 192 F_2 calves were available for analysis.

A complete list of body sizes established on newborn calves and females after first calving is given elsewhere (Meijering and Postma, 1984). Results presented here are on height at withers, depth of chest and width at hips only, as these dimensions were considered representative for the others.

Statistical procedures

Quantitative traits (gestation length, weights, sizes) were analysed by the ordinary least-squares method (Harvey, 1977). Data on ease of calving were analysed by generalized linear model procedures for ordered categorical variates (Bock, 1975; McCullagh, 1980), using a logistic distribution function. After rearranging the data into contingency tables of order $p \times 3$, where the p rows represent specific factor combinations and the three columns are the categories of response, the probability of response in the kth category and the jth row was assumed to be

$$P_{jk} = F(t_k - \mu_j) - F(t_{k-1} - \mu_j),$$

where μ_j = location parameter for row j, composed of general mean, main effects and interactions,
t_k = fixed threshold, with $t_0 = -\infty < t_1 = 0 < t_2 < t_3 = \infty$,
F = logistic cumulative distribution function with mean 0 and variance $\pi^2/3$.

This type of model is commonly referred to as a threshold model, where an underlying unobservable continuous liability variate is assumed to respond in the observable scale by a set of fixed thresholds (e.g. Falconer, 1983). Parameters (including t_2) were estimated by means of the maximum likelihood procedure under sum to zero restrictions. The likelihood was maximized with an iterative algorithm programmed in GENSTAT (GENSTAT, 1977). Estimates for (asymptotic) (co)variances of the estimators were obtained from Fisher's information matrix. Only reduced models were fitted and compared hierarchically by means of the likelihood ratio test. The goodness of fit of the models with respect to the saturated product-multinomial model was examined by Pearson's chi-square statistic. In a conceptual and an operational sense the procedure is closely related to the method of breeding value estimation for categorical variates, as proposed by Gianola and Foulley (1983) and Harville and Mee (1984).

Models

Factors examined with respect to their influence on birth traits of F_1 calves were breed, sire group, sex of calf, season of birth (calendar trimester) and parity of dam (first, second, $\geqslant$ third). Final models selected were:

gestation length: $y_{ijklmn} = \mu + b_i + s_j + g_k + t_l + p_m + (bg)_{ik} + (tp)_{lm} + e_{ijklmn}$

birthweight: $y_{ijkmn} = \mu + b_i + s_j + g_k + p_m + (bs)_{ij} + e_{ijkmn}$

calf sizes: $y_{ijkmn} = \mu + b_i + s_j + g_k + p_m + e_{ijkmn}$

ease of birth: $\mu_{ijkm} = \mu + b_i + s_j + g_k + p_m + (bg)_{ik}$;

where y_{ijklmn} = $ijklmn$th observation

μ_{ijkm} = location parameter for the subpopulation defined by breed i, sex j, sire group k and parity m;

μ = overall mean;

b_i = effect of breed i ($i = 1, 2, 3$; 1 = HF, 2 = DRW, 3 = DF);

s_j = effect of sex j ($j = 1, 2$; 1 = male, 2 = female);

g_k = effect of sire group k ($k = 1, 2$; 1 = L, 2 = H);

t_l = effect of season l ($l = 1, \ldots, 4$; 1 = Jan.—Mar., . . . , 4 = Oct.—Dec.);

p_m = effect of parity m ($m = 1, 2, 3$; $3 = \geqslant$ 3rd);

e_{ijklmn} = residual.

Weights and sizes of F_1 females during rearing and after first calving were analysed by age class c ($c = 3, 6, 9, 12, 15$ or 25 months) by the model:

$$y^c_{ikmno} = \mu + b_i + g_k + p_m + b(x^c_{ikmno} - \bar{x}^c) + e_{ikmno}$$

where y^c_{ikmno} = $ikmno$th observation for age class c;

μ, b_i, g_k, p_m, e_{ikmno} are as defined;

ys_n = effect of the combination year-season of birth n ($n = 1, \ldots, 9$; 1 = Oct.—Dec.'78, . . . , 9 = Jul.—Sep.'81);

b = regression coefficient;

x^c_{ikmno} = age of $ikmno$th animal in age group c (days);

$\bar{x}^c$ = average age in age group c.

Factors examined for their influence on birth traits of F_2 calves were breed, sex of calf, maternal grandsire group, sire group and season of birth. Final models selected were:

gestation length: $y_{ijklm} = \mu + b_i + s_j + mgg_k + sg_l + e_{ijklm}$

birthweight: $y_{ijklm} = \mu + b_i + s_j + mgg_k + sg_l + (bs)_{ij} + e_{ijklm}$,

ease of birth: $\mu_{ijkl} = \mu + b_i + s_j + mgg_k + sg_l + (b.mgg)_{ik} + (s.sg)_{jl}$,

where: y_{ijklm}, μ, b_i, s_j, e_{ijklm} are as defined;

μ_{ijkl} = location parameter for subpopulation defined by breed i, sex j, maternal grandsire group k and sire group l;

mgg_k = maternal grandsire group k ($k = 1, 2$; 1 = L, 2 = H);

sg_l = sire group l ($l = 1, 2$; 1 = L*, 2 = H*).

All factors and two-factor interactions not included were not significant ($P > 0.10$). Note that the effects of sire and maternal grandsire groups on ease of birth were estimated in the logistic liability scale. Consequently, additive effects of gene substitutions were assumed to take place in the liability scale rather than in the observable scale. An assumption made implicitly in the fixed model approach is that, as a consequence of truncation selection, variances between sires and maternal grandsires within groups are negligibly small compared to the variances within sires. In the analysis of F_1 records, error covariances due to repeated records (three records at most per cow in the base population) were neglected.

TABLE I

Parameter estimates (± SE) for significant ($P < 0.10$) factors in the final models for birth

Source		N[a]	Ease of birth (SD units)[b]	Gestation length (d)
μ		682	0.67 ± 0.07	279.97 ± 0.24
t_1			0	
t_2			3.25 ± 0.13	
HF		207	0.04 ± 0.09	3.59 ± 0.25
DRW		228	0.13 ± 0.09	−1.17 ± 0.24
DF		247	−0.17 ± 0.08	−2.42 ± 0.24
♂♂		336	0.34 ± 0.06	1.08 ± 0.17
♀♀		346	−0.34 ± 0.06	−1.08 ± 0.17
L-sires		358	−0.23 ± 0.06	−0.59 ± 0.17
H-sires		324	0.23 ± 0.06	0.59 ± 0.17
Season 1		186		−0.81 ± 0.34
2		274	c	0.33 ± 0.31
3		64		0.45 ± 0.59
4		158		0.04 ± 0.36
Parity 1		158	1.00 ± 0.10	−0.69 ± 0.39
2		174	−0.38 ± 0.09	0.26 ± 0.34
⩾3		350	−0.62 ± 0.08	0.42 ± 0.28
HF ♂♂		98		
♀♀		109		
DRW ♂♂		111		
♀♀		117		
DF ♂♂		127		
♀♀		120		
HF L		110	0.21 ± 0.09	0.32 ± 0.25
H		97	−0.21 ± 0.09	−0.32 ± 0.25
DRW L		119	−0.34 ± 0.09	−0.64 ± 0.24
H		109	0.34 ± 0.09	0.64 ± 0.24
DF L		120	0.13 ± 0.08	0.33 ± 0.23
H		118	−0.13 ± 0.08	−0.33 ± 0.23
Parity ×	Season			
1	1	38		−1.26 ± 0.54
2	1	58		0.73 ± 0.48
⩾3	1	90		0.53 ± 0.42
1	2	72		−0.55 ± 0.48
2	2	72		0.90 ± 0.45
⩾3	2	130		−0.35 ± 0.37
1	3	6		2.81 ± 0.99
2	3	11		−1.62 ± 0.84
⩾3	3	47		−1.19 ± 0.67
1	4	42		−1.00 ± 0.54
2	4	33		−0.00 ± 0.53
⩾3	4	83		1.01 ± 0.43

[a] Number of observations (approximate for dimensions).

[b] $SD = \pi/\sqrt{3}$.

[c] Not in final model.

traits of F_1 calves

Birth weight (kg)	Wither height (cm)	Chest depth (cm)	Hip width (cm)
40.33 ± 0.18	73.34 ± 0.11	27.44 ± 0.07	16.63 ± 0.05
4.04 ± 0.24	3.67 ± 0.15	1.43 ± 0.10	0.25 ± 0.06
−0.75 ± 0.24	−2.42 ± 0.15	−0.71 ± 0.10	0.08 ± 0.06
−3.29 ± 0.24	−1.24 ± 0.14	−0.72 ± 0.09	−0.33 ± 0.06
1.54 ± 0.17	0.56 ± 0.10	0.21 ± 0.07	0.19 ± 0.04
−1.54 ± 0.17	−0.56 ± 0.10	−0.32 ± 0.07	−0.19 ± 0.04
−1.34 ± 0.17	−0.48 ± 0.10	−0.28 ± 0.07	−0.18 ± 0.04
1.34 ± 0.17	0.48 ± 0.10	0.28 ± 0.07	0.18 ± 0.04
−3.09 ± 0.27	−0.10 ± 0.17	−0.90 ± 0.11	−0.50 ± 0.07
0.74 ± 0.26	0.16 ± 0.16	0.26 ± 0.10	0.15 ± 0.07
2.35 ± 0.22	0.95 ± 0.14	0.64 ± 0.09	0.34 ± 0.06
0.50 ± 0.24			
−0.50 ± 0.24			
−0.64 ± 0.24			
0.64 ± 0.24			
0.15 ± 0.23			
−0.15 ± 0.23			

RESULTS

Birth traits of F_1 calves

Estimates for the parameters corresponding with the significant ($P < 0.10$) factors in the final models are presented in Table I. The factor of main interest is sire group, as it indicates the significance of (correlated) responses to sire selection by direct genetic merit. For ease of birth, sire group interacted significantly with breed, indicating variation among breeds in selection responses. Contrasts between sire groups (L minus H) were estimated as -0.04 ± 0.22 ($P = 0.87$), -1.15 ± 0.21 ($P = 0.00$) and -0.21 ± 0.20 ($P = 0.29$) units in the underlying (logistic) scale for the HF, DRW and DF breeds, respectively. So only in the DRW breed did sire selection yield a significant difference in responses. In Table II, the corresponding relative frequency estimates for the three categories of response are given at the level of first parity dams, averaging over sexes. The variation in observed responses among breeds is probably due to differences in realized selection intensities, because selection of sires often had to be based on rather scanty information because of deficient birth-recording programmes up to and during the initial years of the trial. Additional factors of significant influence on ease of birth were sex of calf and parity of dam, but not season of birth. The parameter estimates show the well-known tendency towards a greater difficulty in male calves and in first parity cows. In the underlying scale, sire group did not interact ($P > 0.10$) with either of these factors, nor did they interact significantly with one another.

For gestation length, sire-group-by-breed interaction was significant as well. Contrasts between sire groups (L minus H) were -0.54 ± 0.60 ($P = 0.37$), -2.46 ± 0.58 ($P = 0.00$) and -0.52 ± 0.55 ($P = 0.34$) days for the HF, DRW and DF breeds, respectively. Additional factors of significance were sex of calf (a difference of 2.16 ± 0.34 days between males and females) and parity-by-season interaction. The latter interaction seems to have been caused by rather erroneous results in the third trimester, due to small numbers of observations.

TABLE II

Estimated frequencies for ease of birth categories in F_1 calves by breed and sire group at the first-parity level, averaging[a] over sexes

	L sires			H sires		
	Easy	Normal	Difficult	Easy	Normal	Difficult
HF	16.1	66.0	17.9	15.6	65.9	18.5
DRW	23.2	64.6	12.2	8.9	61.3	29.8
DF	20.3	65.6	14.1	17.3	66.1	16.6

[a] Probabilities for each sex were computed separately and averaged in the original scale.

For birthweight, sire group did not interact significantly ($P > 0.10$) with the other factors examined. The contrast between sire groups was −2.68 ± 0.34 kg. In addition, sex of calf and breed-by-sex interaction were significant sources of variation. Birthweight increased significantly with parity of dam. Differences between sexes were larger in the HF and DF breeds (4.08 ± 0.60 and 3.38 ± 0.56 kg, respectively) than in DRW (1.80 ± 0.58 kg). Except for absence of significance of breed-by-sex interaction and breed-specific differences in single measurements, parameter estimates for calf size corresponded well with those observed for birthweight.

Body development of F_1 females

The significance of the various factors in the final model for weight and (selected) measurements of F_1 females at 3, 6, 9, 12, 15 and 25 months of age is indicated in Table III. Though significant at birth, sire group was not a factor of importance ($P > 0.10$) for any of the traits considered between 3

TABLE III

Significance (P-values) of factors in the model for weights and sizes of F_1 females at ages 3, 6, 9, 12, 15 and 25 months

Source	3 months				6 months			
	BW[b]	WH	CD	HW	BW	WH	CD	HW
Breed	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.87
Sire group	0.43	0.33	0.90	0.50	0.10	0.57	0.23	0.28
Parity of dam	0.00	0.01	0.00	0.04	0.08	0.05	0.00	0.06
Year—season of birth	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Regression[a]	0.12	0.24	0.20	0.46	0.00	0.00	0.00	0.00
	9 months				12 months			
Breed	0.01	0.00	0.00	0.14	0.00	0.00	0.00	0.00
Sire group	0.82	1.00	0.28	0.62	0.45	0.73	0.83	0.45
Parity of dam	0.09	0.01	0.00	0.00	0.04	0.00	0.00	0.00
Year—season of birth	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Regression[a]	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	15 months				25 months			
Breed	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Sire group	0.03	0.52	0.36	0.59	0.02	0.10	0.26	0.56
Parity of dam	0.66	0.01	0.55	0.09	0.41	0.53	0.51	0.54
Year—season of birth	0.00	0.00	0.00	0.00	0.00	0.23	0.28	0.00
Regression[a]	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[a] On age within age group.

[b] BW = bodyweight; WH = height at withers; CD = depth of chest; HW = width at hips.

and 12 months of age. At 15 and 25 months of age body weight, but none of the size measurements, differed significantly between sire groups. The contrast between sire groups (L minus H) for weight was maximum at 25 months (10 days after calving): −10.8 ± 4.7 kg. Relative to the overall mean, this amounted to only 2.3%. Contrasts for all four traits from birth up to an average age of 25 months are shown in Fig. 2. Up to 12—15 months of age parity of dam was a factor of significance ($P < 0.10$) for body weight and dimensions: progeny of first parity dams were markedly smaller during the first year of the rearing period.

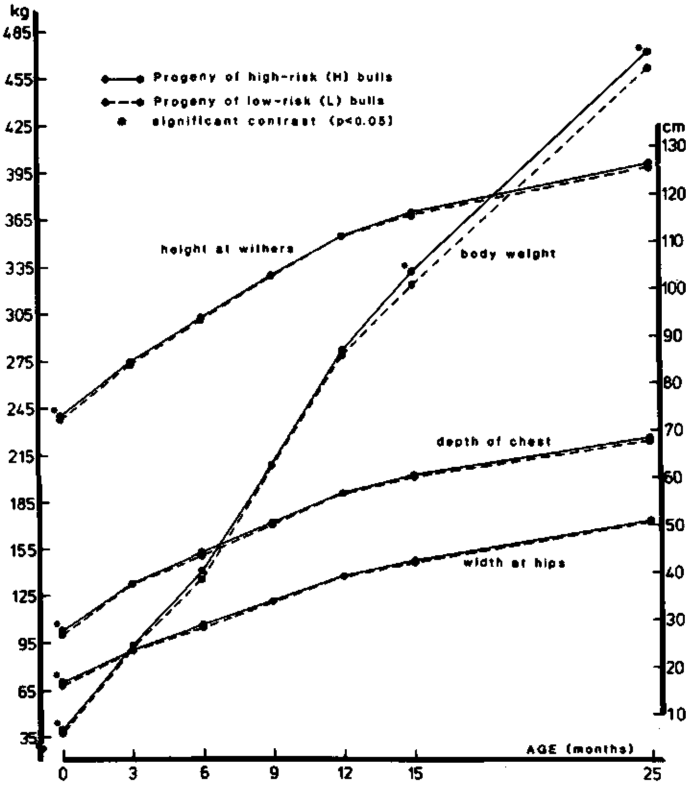


Fig. 2. Body weights and sizes of F_1 females (means + least squares constants) by age and sire group.

Birth traits of F_2 calves

Table IV summarizes the parameter estimates for the factors with significant ($P < 0.10$) effect on ease of birth, gestation length and birthweight of F_2 calves. The factor of main interest here is the maternal grandsire group (mgs group). The contrasts between mgs groups reflect the responses due to maternal grandsire merit obtained indirectly through

TABLE IV

Parameter estimates (± SE) for factors with significant ($P < 0.10$) effect on birth traits of F_2 calves

Source	Number of observations	Ease of birth (SD units)	Gestation length (d)	Birthweight (kg)
μ	197	0.98 ± 0.14	279.27 ± 0.32	38.00 ± 0.33
t_1		0		
t_2		2.96 ± 0.22		
HF	65	−0.14 ± 0.17	2.89 ± 0.45	2.83 ± 0.46
DRW	61	0.19 ± 0.17	−0.91 ± 0.46	−0.26 ± 0.47
DF	71	−0.04 ± 0.16	−1.99 ± 0.44	−2.57 ± 0.45
L mgs[a]	106	−0.34 ± 0.12	−0.79 ± 0.33	−0.92 ± 0.34
H mgs	91	0.34 ± 0.12	0.79 ± 0.33	0.92 ± 0.34
L* sires	102	−0.34 ± 0.12	−0.85 ± 0.33	−0.68 ± 0.34
H* sires	95	0.34 ± 0.12	0.85 ± 0.33	0.68 ± 0.34
♂♂	102	0.63 ± 0.13	0.70 ± 0.33	1.39 ± 0.33
♀♀	95	−0.63 ± 0.13	−0.70 ± 0.33	−1.39 ± 0.33
HF L	38	−0.46 ± 0.17		
H	27	0.46 ± 0.17	[b]	
DRW L	35	−0.01 ± 0.17		
H	26	0.01 ± 0.17		
DF L	33	0.47 ± 0.17		
H	38	−0.47 ± 0.17		
HF ♂♂	35			1.19 ± 0.47
♀♀	30			−1.19 ± 0.47
DRW ♂♂	29			−0.01 ± 0.47
♀♀	32			0.01 ± 0.47
DF ♂♂	38			−0.18 ± 0.46
♀♀	33			0.18 ± 0.46
L* ♂♂	54	−0.32 ± 0.12		
♀♀	48	0.32 ± 0.12		
H* ♂♂	48	0.32 ± 0.12		
♀♀	47	−0.32 ± 0.12		

[a] mgs = maternal grandsire group.

[b] Not in final model ($P > 0.10$).

selection of sires by direct genetic merit for calving ease. For instance in a genetic model comprising a direct genetic component only, these contrasts are expected to be half of those observed for F_1 calves. For ease of birth, mgs group interacted significantly with breed. Contrast estimates (L minus H) were −1.59 ± 0.43 ($P = 0.00$), −0.70 ± 0.43 ($P = 0.10$) and 0.25 ± 0.39 ($P = 0.51$) units in the underlying scale for the HF, DRW and DF breeds, respectively. Except for DF, the direction of the contrasts between mgs groups corresponded to those observed for sire groups in F_1 calves. Comparison of sizes and significances of sire-group contrasts for ease of birth in F_1 calves and mgs-group contrasts in F_2 calves shows, however, that the HF breed, not the DF, was out of line. This is also obvious from the estimated frequencies in Tables II and V. In F_2 calves, sire group (L*, H*) did not interact with breed, so that selection of bulls to serve the F_1 females seemed to have been equally successful in each breed. Sire group did not interact significantly with mgs group either, so that direct genetic merit of one group of sires and maternal grandsire merit of a second group seem to behave additively. In contrast to F_1 calves, sire group showed a significant interaction with sex of calf, the contrast between males and females being much larger (1.90 ± 0.34 units; $P = 0.00$) in calves sired by H* bulls than in those sired by L* bulls (0.61 ± 0.35 units; $P = 0.08$).

For gestation length of F_2 calves, the factors breed, mgs group, sire group and sex, but none of their interactions, were significant ($P < 0.10$). The contrast between mgs groups (L minus H) was −1.58 ± 0.66 days ($P = 0.02$). Note that in F_1 calves the contrast between sire groups for gestation length was breed-dependent. Second-generation progeny of L sires also had significantly lower birthweights (−1.84 ± 0.68 kg; $P = 0.01$). Both for gestation length and birthweight, the direction of the contrast between mgs groups conformed with the one observed for sire groups in F_1 calves.

TABLE V

Estimated frequencies for ease of birth categories in F_2 calves by breed and maternal grandsire group (at the first-parity level), averaging[a] over sire groups and sexes

	L mgs[b]			H mgs		
	Easy	Normal	Difficult	Easy	Normal	Difficult
HF	49.6	43.6	6.8	18.7	57.5	23.8
DRW	33.0	54.0	13.1	20.4	57.6	22.0
DF	28.1	56.0	15.9	33.1	53.9	13.0

[a] Probabilities for each sex by sire group subclass were computed separately and averaged in the original scale.

[b] mgs = maternal grandsires.

DISCUSSION

Selection experiments with cattle are prone to be hampered by the long generation interval and physical contraints. In general, these limitations lead to trials with few generations, without replicates and with small numbers of animals per line. The present study, though not a selection trial in the real sense, suffered from the same limitations. Particularly the number of complete birth records from F_2 calves was less than desirable, a situation aggravated by the interaction between breed and group of sire of F_1 calves for ease of birth and gestation length. As selection intensities were not exactly known, first-generation responses had to serve as a control for those observed in the second generation. Since first-generation responses for the trait of main interest, i.e. ease of birth, were basically absent in the Black and White breeds, the size of the data set to test the main hypothesis was virtually reduced to the DRW subset. In DRW, in terms of units of the (logistic) liability scale, sire selection yielded a contrast (L minus H) of -1.15 ± 0.21 between F_1 progeny of low-risk and high-risk sires, irrespective of parity. The corresponding difference in estimated frequencies of difficult births at the first-parity level was -17.6%. In the second generation, a contrast of -0.70 ± 0.43 was observed between these (now maternal grandsire) groups, corresponding with -8.9% difficult births. The identity of sign of these figures suggests a positive relationship between direct and maternal grandsire merits for ease of birth. This observation is supported by the mostly positive correlation estimates in field data ($r \cong 0.25$; Pollak and Freeman, 1976; Gaillard, 1980; Dwyer and Schaeffer, 1984), in spite of the negative estimates for the correlation between direct and (pure) maternal effects. Obviously, the regression of maternal grandsire merit on direct genetic merit is positive, and, returning to the expression for the regression coefficient given in the introduction, $r_{DM} > -\sigma_D/2\sigma_M$. The size of the contrast between mgs groups is, however, somewhat larger than expected on the ground of the parameter estimates given by Thompson et al. (1981) and Dwyer and Schaeffer (1984). The insignificant contrasts between L and H sires of DF origin in both the first and the second generation, and the erroneous results in this respect for the HF group, neither support nor contradict the conclusion from the DRW data and from the mentioned literature.

The results from this study, supported by correlation estimates in field data, lead to the conclusion that the hypothesis that low-risk bulls sire small calves, which develop into small heifers and which in turn calve with more difficulty, has to be rejected as a whole. Low-risk bulls did sire smaller calves born after shorter gestations than high-risk bulls (Tables I and IV). Differences in body development between the two progeny groups were consistent but minor, however, at every stage of the rearing period and after first calving (Fig. 2). Since the relationships between calving ease and dam size were generally found to be very weak (Hässig, 1979; Meijering and Postma, 1984), it is unlikely that the differences in ease of birth between F_2 progeny of low-risk and high-risk sires were to any major extent due to a difference in average heifer size.

The contrasts observed for birthweight between the L and H sire and maternal grandsire groups in the first and second generation, respectively, suggest a rather strong positive correlation between direct and maternal grandsire merits for calf size. This observation is supported by an estimate reported by Gaillard (1980): $r_{s,mgs} = 0.78$. Since maternal grandsire merits for birthweight and ease of birth show a moderate positive correlation ($r_g \approx 0.65$) and (pure) maternal heritability of birthweight is extremely low ($h^2 \approx 0.02$; Philipsson, 1976; Gaillard, 1980), one might conjecture that the maternal grandsire effect on ease of birth is dominated by direct inheritance of cattle size, where calf size at birth is one principal component.

A more likely alternative hypothesis would then be: low-risk bulls sire small calves, which may develop into somewhat smaller heifers, but these are not likely in turn to calve with more difficulty, since low-risk bulls give small second-generation progeny. If this hypothesis is true, a predominant use of low-risk bulls over all parities may, in the long run, lead to a population showing less body development. If used on maiden heifers only, such an effect is unlikely.

CONCLUSION

The hypothesis that second-generation progeny of bulls with low risk for dystocia are born with greater difficulty than those of high-risk bulls, because low-risk bulls sire smaller daughters, is not supported by the results of the present study. There is more evidence that, except for size of daughters, the reverse is true. The favourable impact by the pathway ***direct genetic merit for small calf size → maternal grandsire merit for small calf size → maternal grandsire merit for less difficulty at birth*** seems to outweigh any unfavourable effect by the pathway ***direct genetic merit for small calf size → direct genetic merit for small heifer size → negative maternal effect on ease of birth***. So, from the viewpoint of calving ease of female progeny, there seems to be no ground for reluctance to the use of low-risk bulls for mating heifers.

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RESUME

Meijering, A. et Postma, A., 1985. Réponses a la sélection des taureaux sur les difficultés de naissance. *Livest. Prod. Sci.*, 13: 251—266 (en anglais).

L'hypothèse selon laquelle "Les taureaux à faible risque de dystocie engendrent des veaux petits qui deviennent des génisses petites vêlant plus difficilement" a été testée dans un essai de sélection divergente des taureaux avec des bovins Holstein (HF), Pie-rouge néerlandais (DRW) et Frisons (DF) élevés en race pure. A partir du catalogue d'index, on a choisi des taureaux à faible (L), et à fort (H) risque pour produire les veaux F_1. On a enregistré les caractéristiques de naissance (facilité de naissance, durée de gestation, poids et mensurations) des veaux F_1 et le développement corporel des femelles F_1. A l'intérieur de chaque groupe de descendants paternels, les génisses ont été à leur tour accouplées avec des taureaux à faible (L*) ou à haut (H*) risque. Les caractéristiques de naissance des veaux F_2 ont été enregistrées. On a analysé les variables quantitatives et discrètes respectivement par un modèle habituel des moindre-carrés et par un modèle linéaire généralisé.

Les différences entre descendances pour les facilités de naissance et la durée de gestation des veaux F_1 n'ont été significatives ($p < 0,10$) que pour la race DRW; pour le poids et les mensurations à la naissance, il n'y a pas eu de telles interactions race x descendance.

Les femelles issues des taureaux L et H n'ont montré que des différences mineures entre elles pour le développement corporel au cours de la croissance et après le premier vêlage. Les influences des grands-pères maternels (L par rapport à H) et des pères (L* par rapport à H*) sur les caractéristiques de naissance des veaux F_2 ont été significatives et additives. Cependant l'effet du grand-père maternel sur les facilités de naissance n'a pas été significatif dans la race DF. Dans la race DRW, l'égalité des signes des comparaisons (combinaisons linéaires) entre groupes de pères des veaux F_1 et de celles entre groupes de grands-pères maternels des veaux F_2 confirme la conclusion des études de terrain selon laquelle la valeur génétique directe et la valeur génétique du grand-père pour la facilité de naissance sont corrélées positivement. Cette conclusion n'est ni confirmée ni infirmée par les résultats en race pie noire (HF et DF). En conclusion, l'hypothèse présentée au début doit être rejetée et on peut supposer que l'influence du grand-père sur les facilités de naissance est dominée par l'hérédité directe de la taille du veau.

KURZFASSUNG

Meijering, A. und Postma, A., 1985. Erfolge der Bullenselektion auf Schwergeburten. *Livest. Prod. Sci.*, 13: 251—266 (auf englisch).

In einem zweiseitigen Reinzucht-Selektionsversuch mit Holstein Friesian (HF), Niederländischen Rotbunten (DRW) sowie Niederländischen Schwarzbunten (DF) wurde die Hypothese getestet, dass Bullen, die mit einem geringen Risiko Schwergeburten vererben, kleine Kälber zeugen die sich dann zu kleinen Färsen entwicklen, und nachher grössere Schwierigkeiten beim Abkalben haben. Die Auswahl der Bullen mit geringem (L) oder hohem (H) Risiko der Schwergeburtenvererbung erfolgte anhand der Vererbungsdaten. Die Geburtsmerkmale (Leichtkalbigkeit, Trächtigkeitsdauer, Gewicht und Körpermasze) der F_1 Kälber aus die Versuchsbaarungen aufgezeichnet ebenso wie die körperliche Entwicklung der weiblichen F_1 Tiere. Innerhalb der Väter-Gruppen wurden die weiblichen F_1 Tiere der Reihe nach sowohl an Bullen mit geringem (L*) als auch hohem (H*) Risiko der Schwergeburtenvererbung angepaart. Auch für die F_2 Kälber wurden die Geburtsmerkmale dokumentiert. Die quantitativen und kategorischen Merkmale wurden mit normalen Least-Squares Programm bzw. mit einem generalisierten linearen Modell berechnet.

Nur für die DRW Rasse waren die Unterschiede zwischen den Väter-Gruppen für die Merkmale Leichtkalbigkeit und Trächtigkeitsdauer der F_1 Kälber signifikant ($P < 0.10$); für das Gewicht des Kalbes und seine Körpermasze gab es jedoch keine derartige Interaktion zwischen Rasse und Väter-Gruppe Weibliche F_1 Tiere, die von L und H Bullen abstammten, zeigten nur geringe Unterschiede in der körperlichen Entwicklung während der Aufzucht und nach dem ersten Kalben. Der Einfluss sowohl der mütterlichen Grossväter-Gruppe (L im Vergleich zu H) als auch der Väter-Gruppe (L* im Vergleich zu H*) war für die Geburtsmerkmale der F_2 Kälber zignifikant sowie additiv. Für die DF Rasse konnte jedoch kein signifikanter Einfluss der mütterlichen Grossväter-Gruppe auf das Merkmal Leichtkalbigkeit festgestellt werden. Die Gleichheit der Vorzeigen in der DRW Rasse für die Differenz der Väter-Gruppen bei den F_1 - und der mütterlichen Grossväter-Gruppen bei den F_2 -Kälbern bestätigt das aus Felddaten stammende Ergebnis, dass der direkte und der durch den mütterlichen Grossvater bedingte genetische Fortschritt im Merkmal Leichtkalbigkeit positiv korreliert sind. Diese Schlussfolgerung wurde durch die Ergebnisse der Schwarzbunten Rassen weder bestätigt noch widerlegt. Aufgrund der Ergebnisse scheint es angezeigt, die oben aufgestellte Hypothese zu verwerfen und es wird vermutet, dass der Einfluss des mütterlichen Grossvaters auf das Merkmal Leichtkalbigkeit durch die direkte Vererbung der Grösse des Kalbes Überlagert wird.

Part IV

SELECTION PROGRAMMES

Chapter 7

Revenues from sire selection for calving traits in Dutch dairy cattle

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The monetary returns from three breeding-bull-selection schemes for calving traits were estimated, viz. identification of low-risk bulls for heifer matings among selected breeding bulls, selection of breeding bulls on direct genetic merit and selection of breeding bulls on maternal grandsire merit. Bulls were assumed to be primarily selected for dairy traits. Calving traits and dairy traits were assumed to be genetically independent. Selection for calving traits was on indices with breeding value estimates for calving ease score, birth weight and gestation length as index traits and dystocia liability, birth weight and gestation length as traits in the breeding objective. Marginal returns from traits in the breeding objective were discounted by factors computed by the gene-flow method. Correlated responses in maternal grandsire effects when selecting for direct genetic effects, and vice versa, were included in these factors by regressing units of genetic superiority. Genetic superiority for dystocia liability was assumed to be expressed in heifers only, while superiority for birth weight and gestation length was supposed to be expressed in heifers and cows. Returns were estimated for several calf price levels and initial incidences of dystocia.

Identification of low-risk bulls among selected breeding bulls proved to increase the returns from a breeding programme in dairy cattle. The reduction in incidence of dystocia in heifers and the associated returns were higher as the initial incidence or the calf price were higher. Breeding value estimates for birth weight and gestation length did not contribute significantly to the accuracy of low-risk bull identification in addition to the estimate for calving ease score when the latter was based on 200 progeny per sire. Selection by indices for direct genetic effects as well as maternal grandsire effects reduced the incidence of dystocia only when calf price was very low (upto about Dfl 5.00 per kg). In the normal calf price range in the Netherlands (Dfl 7.50 - Dfl 15.00 per kg) however, either type of selection should be for an increase in birth weight in spite of a corresponding rise in incidence of dystocia. Because of the reduction of the intensity of selection for dairy traits, the effect of additional selection for birth weight on the total returns from the breeding plan is either negative or only marginally positive however.

According to the concept of genetic pathways involved (MEIJERING, 1984), sires may be evaluated, and subsequently selected, for direct genetic as well as maternal grandsire merits for calving traits (dystocia, stillbirth, birth weight, gestation length). A sire's direct genetic merit is expressed in his progeny when they are born (= mate effect), while the maternal grandsire merit is observed in the progeny of his daughters. In terms of direct and maternal genetic components (KOCH, 1972; WILLHAM, 1972), direct genetic merit refers to the breeding value for the direct genetic component, while maternal grandsire merit incorporates a direct component and a maternal component as well as their interaction. In spite of the negative direct-maternal covariances observed for calving traits (GAILLARD, 1980; THOMPSON et al., 1981; DWYER & SCHAEFFER, 1984; CUE & HAYES, 1985), direct genetic and maternal grandsire merits seem to be positively correlated (POLLAK & FREEMAN, 1976; MEIJERING & POSTMA, 1985). Studies by PHILIPSSON (1979) and HANSET (1981) showed that dystocia may be reduced effectively by sire selection on either type of genetic merit. However, when selection for dystocia is to be included in a breeding plan, the effects on the economic returns have to be considered rather than, or in addition to, the biological responses. In dairy cattle, selection for dystocia will reduce the intensity of selection for dairy traits. Besides, an adverse effect on birth weight is to be anticipated in view of the high genetic correlation between these traits (PHILIPSSON et al., 1979). To justify selection for dystocia from an economical point of view, the monetary returns from a reduction in dystocia should compensate the losses associated with these effects. In this study, the returns from three breeding-bull-selection schemes for calving traits are examined within a breeding plan for dairy cattle.

Alternatives studied

1. Preferential mating of heifers to low-risk bulls for dystocia

In this alternative young bulls are assumed to be evaluated for dairy traits and for direct genetic effect on calving traits. Selection of breeding bulls is based on breeding value estimates for dairy traits only however. Estimates of direct genetic merit for calving traits are used to identify low-risk bulls for dystocia among the breeding bulls selected. Heifers are bred to the low-risk bulls identified. This procedure conforms with the present programme in the Netherlands.

2. Selection of breeding bulls on direct genetic merit for calving traits

Young bulls are evaluated as in alternative 1. Selection of breeding bulls however, is based on breeding value estimates for dairy traits and calving traits. There is no preferential mating of heifers.

3. Selection of breeding bulls on maternal grandsire merit of calving traits

Bulls are evaluated for, and selected on, genetic merit for dairy traits and maternal grandsire merit for calving traits.

General assumptions and procedures

The returns from the selection schemes outlined were studied within the general framework of the present breeding programme in the Netherlands. Herein, young bulls are mated to first-lactation females. Consequently, data available for the estimation of direct genetic merit for calving traits (alternatives 1 & 2) refer to second calvings (MEIJERING, 1985 a). Although it has been suspected that a loss of accuracy with respect to the prediction of dystocia in heifers has to be anticipated then (MEIJERING, 1984; DE ROO et al., 1983) most estimates (GAILLARD, 1980; THOMPSON et al., 1981; CUE & HAYES, 1985) indicate that genetic correlations for calving traits between first and later parities are close to unity. Data for the evaluation of sires for maternal grandsire merit are assumed to be recorded at the first parturition of the daughters resulting from the test inseminations. Both for direct and for maternal grandsire effects selection indices were constructed as detailed in the next sections. The returns and responses from these indices were examined.

Breeding value estimates for dairy traits (milk yield, fat and protein content) were assumed to be combined into the net profit index applied in the Netherlands (DOMMERHOLT, 1979), which has a variation of Dfl 135.00. Based on reports by LINDSTRÖM & VILVA (1977), THOMPSON et al. (1980) and GAILLARD (1980), calving traits and dairy traits were assumed to be genetically uncorrelated. It should be noted that calving traits have been considered in the selection of breeding bulls only: in each of the alternatives sires of bulls, dams of bulls and dams of cows were assumed to be selected for dairy traits.

The construction of an index for direct genetic effects on calving traits was based on the present Dutch birth recording scheme (MEIJERING, 1985 a). Herein, data on ease of birth, stillbirth, birth weight and gestation length from 200-300 progeny per sire are recorded. Index traits considered were the breeding value estimates for these four characters. Although ease of birth and stillbirth are categorical variates, the distribution of breeding values should be approximately normal (RÖNNINGEN, 1975; PHILIPSSON, 1979).

(Co)variances required for the construction of an index of breeding value estimates are:

$$\mathrm{Var}\ (\hat{A}_i) = b_i h_i^2 \sigma_{p_i}^2$$

$$\mathrm{Cov}\ (\hat{A}_i, \hat{A}_j) = 4\ b_i\ b_j\ \sigma_{p_i}\ \sigma_{p_j}\ (r_{p_{ij}} + 1/4\ (n-1)\ r_{g_{ij}}\ h_i\ h_j)\ /n$$

$$\mathrm{Cov}\ (\hat{A}_i, A_k) = b_i\ r_{g_{ik}}\ h_i\ h_k\ \sigma_{p_i}\ \sigma_{p_k}$$

, where $b_i = nh_i^2 / (4 + (n-1)\ h_i^2)$ is the accuracy of breeding value estimation for trait i

$\hat{A}_i$ = estimate of breeding value for trait i

A_k = true genotype for trait k in the breeding objective

n = number of half-sib progeny.

Traits considered in the index for maternal grandsire effects were breeding value estimates for the four traits mentioned based on first-calving records from 100 daughters per sire.

After a preliminary analysis, breeding value estimates for stillbirth were dropped from the indices since these contributed extremely little. In an earlier study (MEIJERING, 1985 a), the usefulness of sire evaluation for stillbirth was already questioned in view of the very small (direct) genetic variance observed.

Breeding objective

The breeding objective for calving traits was defined as:

$T = v_l\ g_l + v_b\ g_b + v_g\ g_g$, where g_l, g_b and g_g are genotypes for dystocia liability, birth weight and gestation length respectively, and v_l, v_b and v_g are the corresponding marginal returns. Note that, in conformity with selection theory for categorical variates based on the threshold concept (MEIJERING, 1986 b), gene substitutions for dystocia were assumed to occur in the conceptual liability scale rather than in the observed categorical scale. When dystocia (or ease of birth) is recorded as an all-or-none trait with incidence $(1-\Phi(t-\mu)$, where $t-\mu$ is the distance between the realized liability (μ) and a fixed threshold (t) in units of the standard normal liability scale and $\Phi(.)$ indicates the normal integral, $v_l = \frac{dv_z \{1-\Phi(t-\mu)\}}{d\mu} = v_z \Phi(t-\mu)$, where v_z = marginal returns from a unit increase in the observed scale and $\Phi(.)$ denotes the normal probability density function (DANELL & RÖNNINGEN, 1981; MUELLER & JAMES, 1984). Since v_l is a function of $t-\mu$, the marginal returns from a unit of liability vary with population incidence. Stillbirth was not considered as a separate trait in the breeding objective. Costs of stillbirth cases associated with dystocia were included in the marginal value of dystocia liability. This definition of the breeding objective implies that selection does not address the fraction of stillbirth cases not associated with dystocia.

As discussed by BRASCAMP (1978), marginal returns from traits included in the breeding objective should be discounted to a fixed point in time. The number of discounted expressions, in the sense of BRASCAMP (1975, 1978), for a trait depends on the number of phenotypic expressions associated with one unit of genetic change, the time lags involved and the interest rate. If the number of discounted expressions is the same for all traits in the breeding objective, discounting will only have a scaling effect on the monetary responses to be expected from selection by the index. The relative weights on the index traits and the biological responses will not be affected. This condition may apply to dairy traits, since the expressions for each of these traits are observed simultaneously. For calving traits such a condition was not assumed, so that the breeding objective can be rewritten as: $T = \delta_z a_z g_l \Phi(t-\mu) + \delta_b a_b g_b + \delta_g a_g g_g$, where a_i and δ_i represent the present marginal value and the number of discounted expressions for trait i, respectively.

Present marginal values

A longer gestation in heifers will extend the rearing period. Based on contracts with central rearing units the costs involved were assessed at Dfl 3.00 per day. In cows a longer gestation results in a longer calving interval. From a study by DIJKHUIZEN (1983) marginal costs were assessed at Dfl 1.00 per day. Assuming 25% heifer calvings, the present marginal value of gestation length was fixed at Dfl 1.50 per dag ($a_g = -1.50$).

In the Netherlands, market prices of young calves are based on body weight and type score. These characters were found to be highly correlated however (LAURIJSEN et al., 1980). Taking this into account, 1982 prices of calves with weights in the normal range (35 to 45 kg) varied between Dfl 8.00 and Dfl 14.00 per kg. However, to enable a wider applicability of the results from this study, the present marginal value of birth weight was treated as a variable ranging from Dfl 0.00 to Dfl 15.00 per kg in steps of Dfl 2.50 (a_b = 0.00, 2.50,...., 15.00).

Costs associated with dystocia arise from several sources (PHILIPSSON, 1976 b; MEIJERING, 1980), as indicated in table I, and will depend on the severity of calving difficulty. In the Dutch birth recording programme ease of calving is scored into four major ordered categories: easy (no or minor assistance), normal (easy pull), difficult (hard pull or veterinary aid) and caesarean/fetotomy. Taking easy and normal calvings as the base level, estimates for the additional costs associated with the dystocia (sub)categories identified are given in table I.

Table I. Estimates of costs by category of dystocia (Dfl per case).

source	category				sources of information
	hard pull	vet. aid	caesarean	fetotomy	
vet. fee	2.25	83.50	338.50	196.50	KNMvD (1981)
labour	24.00	36.00	60.00	48.00	-
stillbirth	4.4 k[1]	8.7 k	-	37.1 k	Meijering & Van Eldik (1981)
reduced milk yield[2]	25.00	25.00	25.00	25.00	-
reduced fertility[3]	10.00	10.00	10.00	10.00	Dijkhuizen (1983)
increased culling[4]	118.00	118.00	118.00	118.00	Dijkhuizen (1980,1983)
total	179.25 + 4.4 k	272.50 + 8.7 k	551.50	397.50 + 37.1 k	

1) k = calf price (Dfl per kg)

2) no specification per category available; based on 3% reduction in yield in the first 3 months of lactation of cows not culled.

3) no specification available; based on a 10 days longer calving interval of cows not culled.

4) no specification available; including reduced milk yield, reduced slaughter value and privation of future income.

Analyses of birth recording data (MEIJERING & VAN ELDIK, 1981; MEIJERING, 1985 a) showed that the frequencies in the subcategories "hard pull" and "veterinary aid" appeared in a ratio of approximately 5 : 1 and that the incidence of fetotomy remained relatively constant at 0.1%, in spite of varying dystocia levels. Let t_1 and t_2 be fixed thresholds in the liability scale seperating normal from difficult calvings and difficult calvings from caesareans/fetotomies, respectively. Under these assumptions, the costs of an "average" case of dystocia (C) can be modelled as a function of calf price (k) and frequencies in the ordered categories:

$$C = \{\Phi(t_2 - \mu) - \Phi(t_1 - \mu)\} \ast \{5/6 \ast (179.25 + 4.4\ k) + 1/6 \ast (272.50 + 8.7\ k)\}$$
$$+ \{0.999 - \Phi(t_2 - \mu)\} \ast 551.50 + 0.001 \ast (397.50 + 37.1\ k).$$

The marginal costs of a liability unit are then:

$$\frac{dC}{d\mu} = \{194.8 + 5.1k\}\phi(t_1 - \mu) + \{356.7 - 5.1k\}\phi(t_2 - \mu)$$

From category frequencies observed in earlier studies (MEIJERING & VAN ELDIK, 1981; MEIJERING, 1985 a), the difference between the thresholds $(t_2 - t_1)$ for the Dutch breeds under the present birth recording system, was assessed at 1.2 standard normal units.

By substituting t_2 in the marginal costs equation by $t_1 + 1.2$, marginal present costs of liability $(-a_z\phi(t-\mu))$ are expressed as a function of incidence and calf price level. Entries chosen for these variates in the present study are given in tabel II.

Table II. Marginal present costs (Dfl) of dystocia liability by dystocia incidence and calf price.

incidence	calf price (Dfl/kg)						
$(100 \ast (1-\Phi(t-\mu)))$	0.00	2.50	5.00	7.50	10.00	12.50	15.00
5	20.80	22.10	23.40	24.70	26.00	27.30	28.60
10	40.80	42.80	44.80	46.80	48.80	50.80	52.80
15	57.20	59.80	62.30	64.90	67.40	70.00	72.50
20	72.40	75.30	78.20	81.10	84.00	86.90	89.80
25	86.40	89.50	92.70	95.80	99.00	102.10	105.20
30	99.80	103.10	106.40	109.70	113.00	116.30	119.60

Numbers of discounted expressions were computed by the gene-flow method developed by HILL (1974) and extended and programmed by BRASCAMP (1978). The method computes the returns from a selection programme which are spread over several years and tiers of the population as:

$$\delta = \sum_t \left(\frac{1}{1+q}\right)^t * \underset{\sim}{m}'(t) * \underset{\sim}{h}, \text{ where}$$

δ= number of discounted expressions per unit of genetic superiority

t= number of years from the base year

q= inflation-free interest rate

$\underset{\sim}{m}'(t)$= vector representing the fraction of superior genes in year t in all age classes of the tier-by-sex subclasses defined

$\underset{\sim}{h}$= vector representing the relative value of the expression of a trait for every age class.

In this study, results refer to a time horizon of 30 years starting from the year of selection of breeding bulls from a batch of young bulls (5th year of age) and a 5% interest rate. The distribution over age classes assumed with respect to effective gene transmission to the next generation by the parent groups distinguished is given in table III.

Table III. Relative distribution of gene transmission over age classes (%)

Parent group	age class												
	1	2	3	4	5	6	7	8	9	10	11	12	13
sires of sires						40.0	40.0	20.0					
sires of dams		17.5				28.9	28.9	16.5	8.2				
dams of sires			22.0	18.0	14.0	11.0	8.0	7.0	5.0	4.0	4.0	4.0	3.0
dams of dams		16.0	17.6	20.2	16.2	10.6	6.8	5.8	2.8	1.8	1.0	0.6	0.6
sires of calves 1)						35.0	35.0	20.0	10.0				
sires of calves 2)		20.0				28.0	28.0	16.0	8.0				
dams of calves 3)		100.0											
dams of calves 4)		25.0	20.0	16.0	13.0	8.0	5.0	4.5	3.0	2.0	1.5	1.0	1.0

1) dystocia; direct effect

2) birth weight and gestation length; direct effect

3) dystocia; maternal grandsire effect

4) birth weight and gestation length; maternal grandsire effect.

Young bulls are assumed to be recruited from 6, 7 and 8 year old breeding bulls in the ratio 40%, 40%, 20% (sires of sires) and from cows of age class 3 and older (dams of sires) in the ratio given by BRASCAMP (1975). Replacement females were supposed to be obtained from young bulls (17.5%), i.e. from test inseminations, and from breeding bulls (82.5%) when these are 6, 7, 8 and 9 years of age in the ratio 35%, 35%, 20%, 10% (sires of dams). Cows of all ages were supposed to contribute to replacement females (dams of dams). Allowance was made however, for the fact that farmers may be less inclined to recruit replacements from 1st (no performance record yet) and 2nd (calves sired by test bulls) dams. The paths of gene transmission discussed so far made up the reproduction matrix for dairy traits. The vector of relative values of expressions ($\underset{\sim}{h}$) for these traits was taken from BRASCAMP (1975). A time correction of 0.37 years was applied to account for the medium lactation yield.

For calving traits, an additional row and column, representing young calves, were added to the reproduction matrix. All elements of the column vector were zero. The row vector contained non-zero elements either in the part representing the transmission of genes from sires to calves, in case of evaluation of direct effects (mating effect), or in the part representing the transmission from dams to calves, in case of evaluation of maternal grandsire effects. The ratio of this procedure is illustrated by figure 1.

According to figure 1, paths to be evaluated with respect to direct genetic effects are:

- sires of calves (accounts for mate effect of the selected breeding bulls)
- sires of sires (accounts for mate effect of sons, grandsons etc.)
- sires of dams (accounts for mate effect of grandsons from daughters, grand-grandsons from granddaughters etc.)

For maternal grandsire effects paths to be evaluated are:

- sires of dams (accounts for expressions observed in calves from daughters, granddaughters from daughters etc.)
- sires of sires (accounts for expressions in calves from granddaughters from sons etc.).

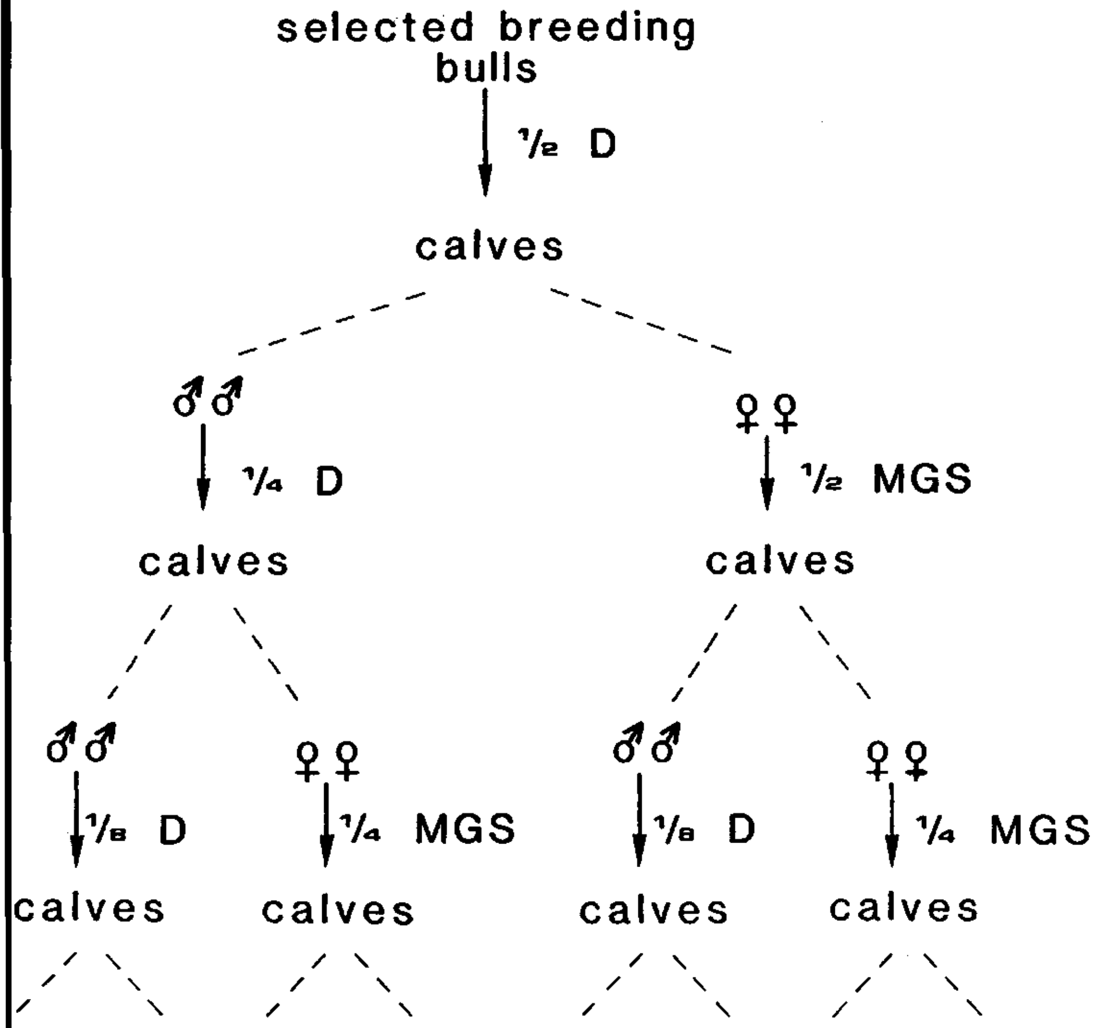

Figure 1. Expression of superiority for direct genetic (D) and maternal grandsire (MGS) effects on calving traits.
(——→ = reproduction with expression; ------- = ageing).

Superiority for dystocia was assumed to be expressed in calves from 1st parity dams only. Since young bulls are tested on cows in first lactation, these calves receive their genes from breeding bulls only. Superiority for birth weight and gestation length on the other hand, was supposed to be expressed in calves from dams of all age classes in a ratio reflecting the age distribution of reproducing females. With respect to these traits, 20% (= fraction of test inseminations) of the calves receive their genetic superiority from young bulls. Discounted expressions for direct genetic effects and maternal grandsire effects were computed independently, and separately for dystocia and birth weight/gestation length.

In each of the four computations the $\underset{\sim}{h}$-vector contained a one in the last position (corresponding with calves of age class 1) and zeros elsewhere, while a time correction of -1 year was applied to account for the fact that calves are zero years old when the expressions occur. For birth weight and gestation length it is assumed implicitly when that genetic correlations between parities are unity and that the relative level of the phenotypic expressions is the same for every age class. A consequence of the procedure followed is that the discounted expressions for dystocia are per 1st parity female and have to be divided by 4 to make them comparable with those for birth weight and gestation length, since 25% of the females were assumed to be of parity 1. Discounted expressions per cow are presented in tabel IV.

Though treated as independent effects, theory and experimental evidence (MEIJERING & POSTMA, 1985) indicate that direct and maternal grandsire effects are positively correlated. In terms of direct (σ^2_m) and maternal (σ^2_m) components of genetic variance and direct-maternal covariance (σ_{dm}), the theoretical regression of breeding value for maternal grandsire effect (A_{mgs}) on breeding value for direct effect (A_d) equals $b_{A_{mgs},A_d} = (\frac{1}{2}\sigma_d + \sigma_{dm})/\sigma^2_d$ while the reverse regression is

$$b_{A_d,A_{mgs}} = (\tfrac{1}{2}\sigma^2_d + \sigma_{dm})/\ (1/4\ \sigma^2_d + \sigma^2_m + \sigma_{dm}).$$

For dystocia, recent estimates of the components involved (THOMPSON et al., 1981; DWYER & SCHAEFFER, 1984; CUE & HAYES, 1985) suggest that both coefficients are in the range 0.10 to 0.25. A value of 0.2 was assumed here, i.e. one unit of superiority for direct genetic effect on dystocia was assumed to be associated with 0.2 units of genetic superiority for maternal grandsire effect and vice versa. Based on parameter estimates by PHILIPSSON (1976 a) and GAILLARD (1980) b_{A_{mgs}, A_d} and $b_{A_d, A_{mgs}}$ for birth weight and gestation length were assessed at 0.35 and 1.75 respectively. The discounted expressions obtained when these correlated responses were accounted for are presented in table IV as "corrected total".

Table IV. Number of discounted expressions (per cow) for dairy traits and calving traits.

	dairy traits	calving traits			
		direct effect		maternal grandsire effect	
path		dystocia	birth weight/ gest. length	dystocia	birth weight/ gest. length
sires of calves	-	0.108	0.345	-	-
sires of sires	0.284	0.069	0.298	0.050	0.166
sires of dams	0.494	0.028	0.120	0.085	0.292
total	0.778	0.205	0.763	0.135	0.458
corrected total		0.232	0.923	0.176	1.793

Parameter estimates

The parameter estimates used in the construction of the index equations for calving traits are given in tables V, VI and VII. Parameters for traits in the direct-effect index were obtained from birth recording data and refer to second calvings. Heritability estimates for birth weight from these data were consistently lower than reported elsewhere (PHILIPSSON et al., 1979). This may be due to the fact that birth weight is estimated by the herdsmen (MEIJERING, 1985 a). Parameters for traits in the maternal-grandsire-effect index refer to first-calf heifers. Heritability of dystocia liability was computed from the heritability of calving ease by the algorithm given by e.g. VINSON et al. (1976).

Table V. Heritability (h^2) and phenotypic variation (σ_p) of calving traits.

Trait	Index				Breeding objective			
	direct effect 1)		maternal grandsire effect 2)		direct effect		maternal grandsire effect	
	h^2	σ_p	h^2	σ_p	h^2	σ_p	h^2	σ_p
calving ease	0.09	0.63	0.10	0.68				
birth weight (kg)	0.13	5.0	0.13	5.0	0.25	5.0	0.13	5.0
gestation length (days)	0.46	5.0	0.15	5.0	0.46	5.0	0.15	5.0
dystocia liability					0.12 3)	1.0	0.12	1.0

1) estimates from Dutch birth recording data (MEIJERING, 1985 a); calving ease scored on a 4-point scale; birth weight estimated.

2) Philipsson et al. (1979).

3) computed from h^2 of calving ease score.

Table VI. Phenotypic (below diagonal) and genetic (above diagonal) correlations for direct genetic effects on calving traits (PHILIPSSON et al., 1979; MEIJERING & VAN ELDIK, 1981; MEIJERING, 1985 a).

	(1)	(2)	(3)	(4)
1. calving ease		0.90	0.50	1.00
2. birth weight	0.35		0.40	0.90
3. gestation length	0.20	0.25		0.50
4. dystocia liability				

Table VII. Phenotypic (below diagonal) and genetic (above diagonal) correlations for maternal grandsire effects on calving traits (PHILIPSSON et al., 1979).

	(1)	(2)	(3)	(4)
1. calving ease		0.65	0.20	1.00
2. birth weight	0.35		0.40	0.65
3. gestation length	0.20	0.25		0.20
4. dystocia liability				

1. Preferential mating of heifers to low-risk bulls

When breeding bulls are selected for dairy traits only, and when dairy traits and calving traits are genetically uncorrelated, selection responses for calving traits are essentially zero. They are actually zero when low-risk bulls and bulls not recommended for heifers contribute to the same extent to the next generation of males and females. Under that condition, revenues from low-risk-bull identification among selected breeding bulls are entirely due to differences in the phenotypic expressions of direct genetic merits for calving traits between heifers and cows. When the phenotypic expressions of direct genetic merit for birth weight and gestation length are assumed to be independent of parity and when bulls identified as "low-risk" yield as many progeny as other breeding bulls, birth weight and gestation length may be dropped from the breeding objective: for these traits it is indifferent then whether a bull is used on heifers or cows. With only dystocia liability left in the breeding objective, the index to be preferred in the identification of low-risk bulls should maximize the response for this trait, or, equivalently, the correlation between index and breeding objective (r_{IH}), with a minimum number of index traits. Dropping the breeding values for birth weight and gestation length from the index for direct genetic effects reduced r_{IH} by only 0.015 (from $r_{IH} = 0.920$ to $r_{IH} = 0.905$). Retaining the breeding value for birth weight or gestation length as the only index trait reduced r_{IH} to 0.84 and 0.39 respectively. It was therefore concluded that the breeding value for calving ease score is the only trait required in a low-risk-bull-identification programme as performed in The Netherlands (about 200 progeny per sire), while this trait may to some extent be replaced by the breeding value for birth weight but not by breeding value for gestation length.

The respons to be expected from the identification of low-risk bulls by the estimate of breeding value for calving ease score equals $-\frac{1}{2}*i*r_{IH}*\sqrt{h_l^2} \approx -i*0.157$ liability units, where h_l^2 is heritability of liability and i relates to the fraction of breeding bulls identified as "low-risk". When the initial incidence of dystocia in heifers is $1 - \Phi(t-\mu)$, the incidence to be expected is $1-\Phi(t- (\mu-0.157*i))$ (MEIJERING, 1985 b).

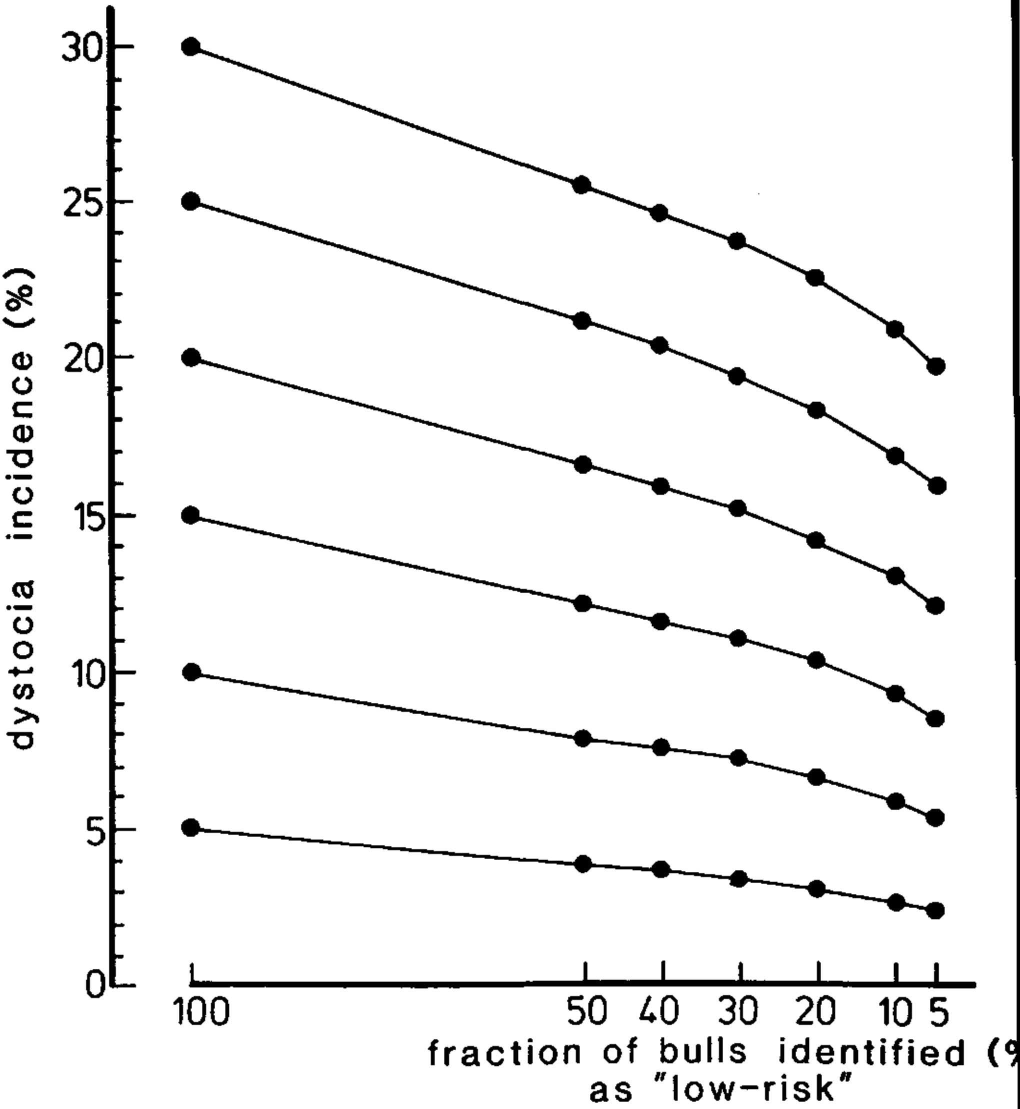

Figure 2. The response in incidence of dystocia in heifers to be expected from the identification of low-risk bulls among selected breeding bulls as a function of initial incidence and fraction of bulls identified.

Figure 2 shows the incidence to be expected as a function of initital incidence and fraction of breeding bulls as "low-risk". Under the threshold model it is evident that preferential mating of heifers to low-risk bulls is more effective when the initial incidence is higher. In computing the monetary returns (MR), the number of discounted expressions used is the one obtained for the path "sires of calves" (table IV) for direct effect on dystocia (0.108 per cow or 0.432 per heifer). The returns were computed as $MR = i \ast r_{IH} \ast\sqrt{h_1^2} \ast 0.432 \ast a_1$ discounted guilders per heifer, where a_1 is the marginal present costs of liability (table II). The discounted returns per heifer by initial incidence and fraction of bulls identified as "low-risk" are shown in figure 3 for calf prices of Dfl 7.50 and Dfl 15.00 per kg. As expected, returns increase with initial incidence and calf price (marginal costs of liability increase), particulary when the fraction of bulls identified is small. It should be noted that these returns are obtained in addition to the returns from selection for dairy traits and that the only costs involved are those of birth recording and sire evaluation for calving ease.

2. Selection of breeding bulls on direct genetic merit for calving traits

In the evaluation of the monetary returns from actual selection of breeding bulls on direct genetic merit for calving traits, the construction of index and breeding objective was as outlined in the relevant sections. By using the initial incidences of dystocia and the calf prices indicated in table II as entries, 42 indices were computed. Discounted marginal returns from liability and birth weight were obtained by multiplying the marginal values in table II by the numbers of discounted expressions for direct genetic effects given as corrected totals in table IV. In each of the indices the discounted marginal returns from gestation length were Dfl -1.38 (0.923 $\ast$ Dfl -1.50). The discounted returns from selection ($i \ast \sigma_I$) by these indices at an intensity of $i = 1$ and the responses obtained with respect to incidence of dystocia (computed from the responses in liability), birth weight and gestation length are shown in figure 4. Starting from a calf of Dfl 0.00, discounted returns per cow first decrease with increasing calf price. However, after reaching a minimum at Dfl 2.50 (for initial incidences $\leq$20%) or Dfl 5.00 (initial incidences $\geq$25%) per kg they almost linearly increase with calf price. The responses indicate that in the range Dfl 0.00 - Dfl 5.00 per kg

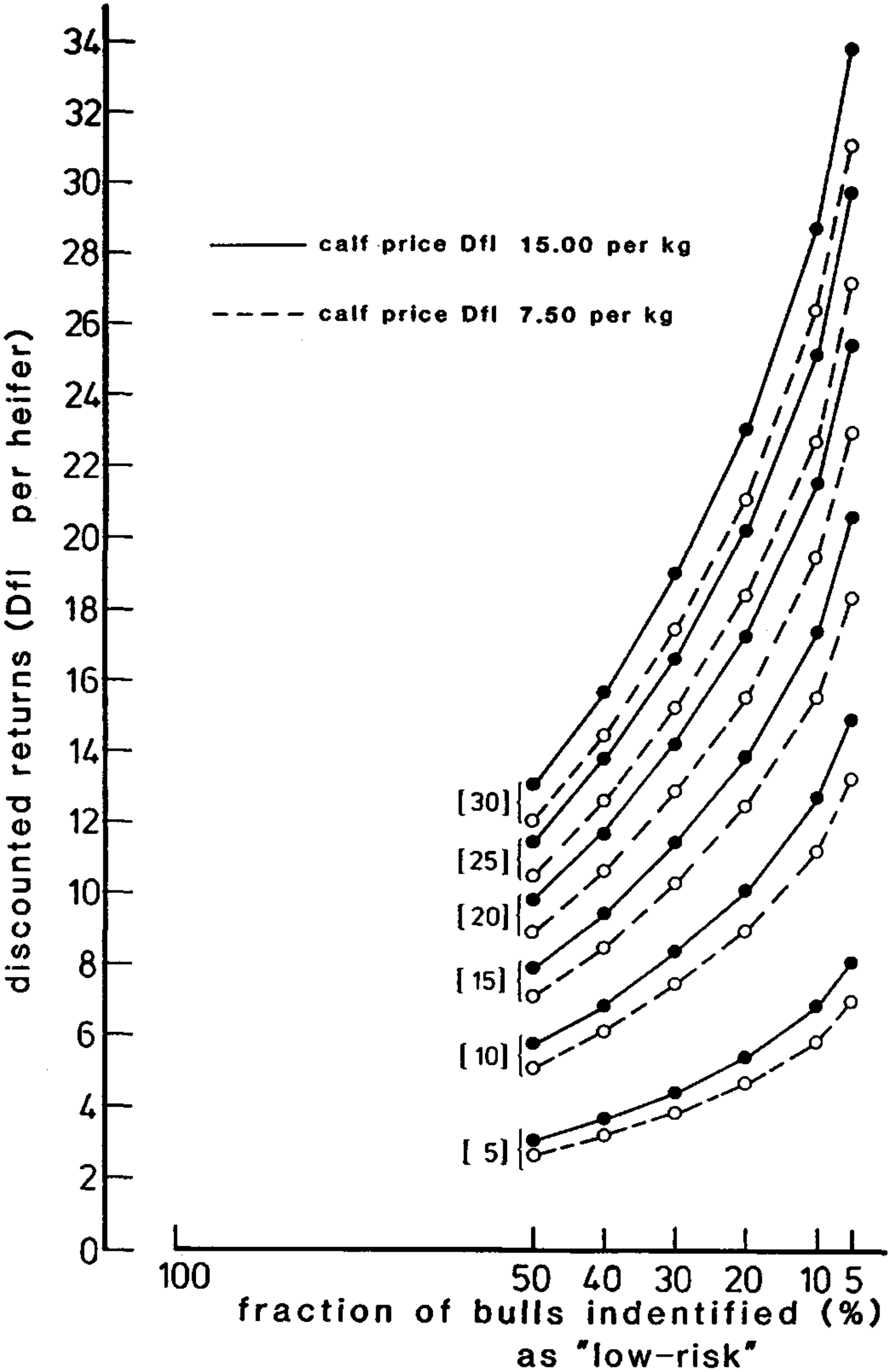

Figure 3. Discounted returns (Dfl per heifer) from the identification of low-risk bulls among selected breeding bulls as a function of initial incidence (between brackets), calf price and fraction of bulls identified.

emphasis on a reduction of dystocia, accompanied by a reduced birth weight, is gradually replaced by an emphasis on an increase in birth weight at the expense of an increase in incidence of dystocia. This is a consequence of the very high positive genetic correlation between dystocia and birth weight and the opposite sign of the respective marginal returns. In the range discussed, the discounted returns from an increase in birth weight are obviously gradually outweighing the discounted costs of dystocia (liability). Since the costs of dystocia liability are positively related to initial incidence of dystocia (table II), it is to be expected that the returns from selection at high initial incidences will be higher than at low incidences before the turning-point, and lower afterwards. From a calf price of Dfl 7.50 onwards the indices almost maximize the response in birth weight.

As gestation length is not very highly correlated to either dystocia or birth weight (table VI), the responses behave somewhat more independenly. Upto a calf price of Dfl 5.00 a negative selection pressure is put on this trait in agreement with its negative marginal value, even though the responses in birth weight and incidence of dystocia are already positive at Dfl 5.00. In that range it contributes considerably to the returns per cow observed (a response of -1.5 days is equivalent to Dfl 4.14 per cow). However, when calf price is higher, the responses gradually become positive due to the genetic correlation with birth weight, while the relative (negative) contribution to the returns per cow is negligible.

Calf prices in the Netherlands are likely to be in the range Dfl 7.50 to Dfl 15.00 per kg. Consequently, from an economical point of view, sire selection for direct genetic effects on calving traits should aim for an increase in birth weight under the assumptions made in this study and should allow the incidence of dystocia to increase as well. Potentially this would yield Dfl 23.00 to Dfl 27.00 per calving cow in terms of discounted returns at a selection intensity of 1 and a calf price of Dfl 15.00. However, selection for calving traits would have to compete with selection for dairy traits. The discounted returns from sire selection for the net profit index for dairy traits (σ_I = Dfl 135.00) are approximately Dfl 105.00 per cow when i = 1. If, for example, the total fraction of young bulls selected is fixed at 10%, the total discounted returns from (independent) selection for dairy traits

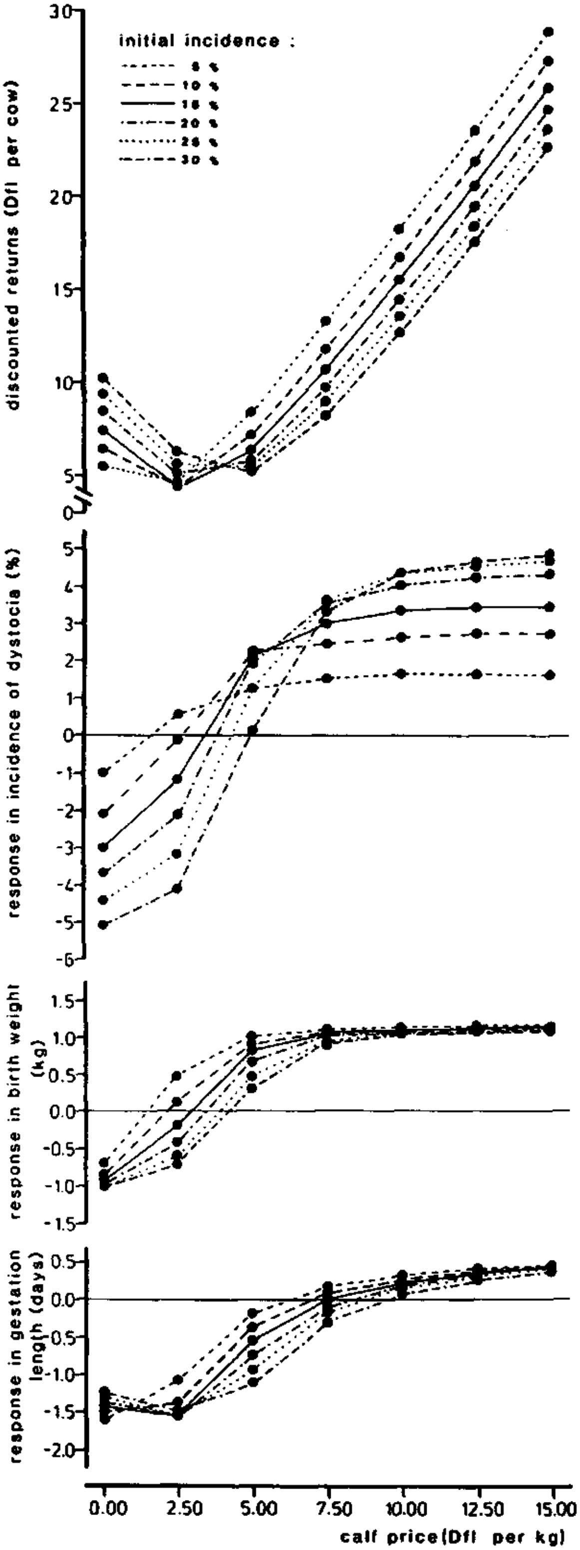

Figure 4. Returns from and responses to sire selection on indices of direct genetic merits for calving traits.

and calving traits (birth weight) at a calf price of Dfl 15.00 per kg would be maximum when the proportions selected for calving traits and dairy traits are about 90% and 11%, respectively. Given these results actual sire selection for direct genetic merit on calving traits is not advisable.

3. Selection of breeding bulls on maternal grandsire merit for calving traits

The discounted returns from sire selection by the indices for maternal grandsire effect on calving traits and the first-generation responses to be obtained when selecting at an intensity of 1 are shown in figure 5. The responses refer to the progeny of daughters of selected sires now. The results obtained are very similar to those observed in the previous section. The minimum in discounted returns as well as the point at which responses become positive is reached at lower calf price level however, while the minimum in returns is more pronounced and the initial incidence of dystocia is of less influence. These features are due to the high discounted marginal returns from birth weight compared with dystocia liability induced by the relatively high number of discounted returns (table IV). As a consequence, the discounted returns per cow obtained after the turning-point, which result from a positive response in birth weight, are higher than by selection for direct effects. The returns amount to about Dfl 37.00 per cow when calf price is Dfl 15.00 per kg. If again the total fraction of young bulls selected is fixed at 10%, this would allow a 60-70% selection for maternal grandsire effect on calving traits (birth weight) i.e. an increase of the proportion selected for dairy traits from 10% to 14-16%. Compared with sire selection for dairy traits only, the gain in total discounted returns per cow would be negligible however.

Discussion

Previous model calculations on the possibilities to reduce dystocia by selection (PHILIPSSON, 1979; HANSET, 1981) focussed on the biological responses to different single-trait-selection strategies, i.e. on the reduction in level of dystocia and the contribution of direct and maternal genetic components therein. From an economical point of view however, any correlated responses with an impact on the returns from the breeding plan should be evaluated as well. In the present study it was attempted to assess the monetary returns from three sire-selection schemes for calving traits when introduced into a breeding plan in which

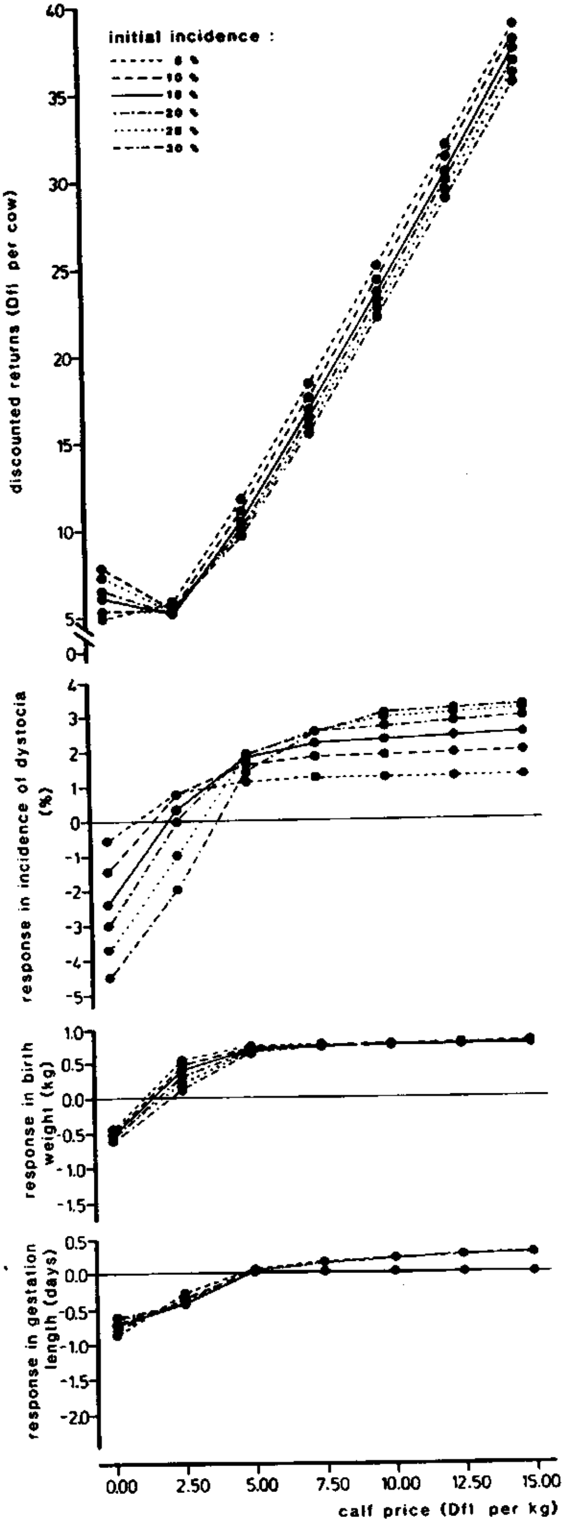

Figure 5. Returns from and responses to sire selection on indices of maternal grandsire merits for calving traits.

sires were selected for dairy traits (milk yield, percentages of fat and protein) only. Returns from responses in birth weight and gestation length were considered in addition to the returns from responses in dystocia (which accounted for stillbirth as well) and compared with the returns from sire selection for dairy traits. Numerous assumptions had to be made which may have influenced the outcome to a more or less serious extent. One of the basic assumptions was the validity of the threshold concept for dystocia, i.e. genetic responses occur primarily in an imaginary standard normal liability scale and are expressed in terms of category frequencies by a change in the argument of the normal integral (MEIJERING, 1985 a). Consequently, responses in liability of similar magnitude will yield smaller responses in the frequency scale at low initial frequencies than when initial frequency is high, as illustrated by figure 2. Since the incidence of dystocia in cows is generally found to be only one third to one fourth of the frequency in heifers, responses in incidence of dystocia in cows are prone to be very small in most populations. In the present study any responses with respect to incidence of dystocia in cows were totally ignored. This may have had little effect in the evaluation of the first alternative, preferential mating of heifers. True, when low-risk bulls are set aside for heifer matings, bulls with more risk are left for cow matings (PHILIPSSON, 1979). However, since the fraction of breeding bulls identified as low-risk will generally be less than 50%, the complementary fraction is too large to elicit any significant response in cows. In the other alternative unjustified neglect of responses in cows will cause an underestimation of the number of discounted expressions for dystocia. With respect to the discounted returns per cow (figures 4 & 5), the effect of a higher number of discounted returns for dystocia is basically equivalent to evaluation of returns at a lower calf price, i.e. the curves representing the returns will shift to the right.

In two other aspects the computation of discounted marginal values of dystocia was not entirely correct. First, important elements of costs of dystocia (reduced milk yield, reduced fertility, increased culling rate) were not specified per category because of lack of information (table II). Since costs associated with these elements are intuitively expected to increase with the degree of difficulty, marginal costs of liability are likely to be somewhat underestimated. This has a similar effect on the returns per cow as underestimation of the number of expressions. Secondly, the gene-flow programme assumes linearity of responses over generations, i.e. each generation the response is assumed to be halved. However, when selection for dystocia is applied, the incidence will change and, due to the dependency on incidence, responses per generation will change in a nonlinear way. When selection is for a reduced incidence the response in a particular generation will be less than half of the one observed in the previous generation, and it will be more than half otherwise. The degree of nonlinearity depends on the intensity of selection. Ignoring this feature causes the number of discounted expressions for dystocia to be biased upwards when dystocia is reduced by selection, and downwards otherwise. Consequently, the estimates of the returns per cow for the alternatives 2 & 3 may be somewhat too optimistic at both sides of the turning-point.

Apart from the factors discussed, the results for the alternatives 2 & 3 are sensitive to the assumptions made with respect to the size of the correlated responses in maternal grandsire effect and direct genetic effect respectively. The coefficients of regression used were based on estimates of components of (co)variance for direct and maternal genetic effects. For dystocia, recent estimates by advanced estimation procedures are available, though limited to the Holstein breed. For birth weight and gestation length however, only two estimates of maternal variance and direct-maternal covariance were available, both obtained by indirect procedures. Although both studies (PHILIPSSON, 1976 a; GAILLARD, 1980) indicate that the maternal genetic variance for these traits is very small compared with the direct genetic variance, the basis for the assumed size of the regression coefficients has to be considered rather weak.

Considering the side-notes made on the evaluation procedure, the results on the alternatives 2 & 3 have to be regarded as indicative: the returns per cow may be somewhat lower than shown by the figures 4 & 5, while in reality the turning-point may be located at a somewhat higher calf price.

Conclusion

Identification of low-risk bulls for dystocia among selected breeding bulls for preferential use on heifers has a favourable impact on the returns from a breeding programme in dairy cattle. The reduction in incidence of dystocia in heifers and the associated returns are higher as the initial incidence or the calf price are higher. When calving ease is recorded as proposed by PHILIPSSON et al. (1979) and sire evaluation is based on a sufficient number of progeny, a linear method (BLUP) of sire evaluation seems to be acceptable (MEIJERING, 1985 a). Additional sire evaluation for birth weight or gestation length does not contribute significantly to the accuracy of identification of low-risk bulls under these conditions.

From an economical point of view, actual sire selection on either direct genetic merit or maternal grandsire merit for calving traits should aim at a reduction of dystocia only when calf price is very low. In the range of prices (Dfl 7.50 - Dfl 15.00 per kg) observed in The Netherlands however, either type of selection should be directed towards an increase in birth weight in spite of an associated rise in incidence of dystocia. Because of the reduction of the intensity of selection for dairy traits, additional selection for birth weight by either type will affect the total returns from the breeding programme negatively or only marginally positively.

Acknowledgment

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SUMMARY

Field data recorded in the early seventies showed that dystocia (calving difficulty) in the main Dutch cattle breeds occurred at a rate of 15-17% in heifers and 5-6% in cows. Corresponding stillbirth rates were 9-12% and 2.5-3.5% respectively. In the sixties and seventies many research papers on dystocia and stillbirth appeared which dealt with frequencies in various breeds and breed crosses, causes, associated factors, economic consequences and factors with systematic impact. These papers are reviewed in chapter 1. Important conclusions can be summarized as follows.

1. Dystocia is a major cause of stillbirth: 40 to 60% of the stillbirth cases encountered in field data are associated with dystocia. Additional negative consequences of dystocia are increased labour and veterinary costs, reduced fertility and milk yield, and an increased culling rate.
2. First-calf heifers and older cows differ both in frequency and in cause of dystocia. The frequency of calving difficulty in heifers is generally three to four times as high as in cows. In heifers, the most frequent cause of dystocia is feto-pelvic-incompatibility, i.e. a disproportion between the size of the calf and the pelvic dimensions of its dam. Deviations in the presentation of the calf account for a second substantial part. In cows, feto-pelvic-incompatibility is encountered less frequently, whereas other causes such as weak labour, uterine torsion and insufficient cervical dilation are relatively more important.
3. Within parity, the probability of dystocia is positively related, i.e. increases, with the weight and dimensions of the calf at birth. The (phenotypic) relationships show a threshold character, i.e. the probability of dystocia increases strongly when the size of the calf exceeds a certain threshold value. The probability of dystocia is positively related with gestation length as well, probably mediated by calf size. With respect to the dimensions of the pelvic inlet of the dam a negative relationship is found. The size of the calf and the dimensions of the dam's pelvic inlet are the basic elements in feto-pelvic-incompatibility.

4. Apart from parity of the dam, factors with systematic influence on the frequency of calving difficulty are sex of calf and season of calving. In male calves the frequency is about twice as high as in females which is mainly due to the larger average size of the males. In the North-Western part of Europe dystocia tends to be more frequent in autumn and early winter than in spring and summer. This seasonal pattern is often, but not always, found to be associated with a seasonal fluctuation in birth weight.
5. Dystocia, stillbirth, as well as the associated calving traits birth weight and gestation length, are influenced by the genotype of both the calf and its dam, which results in a complicated genetic model. With a view to sire selection, the influence of the genotype of the calf is generally referred to as sire-of-calf effect, direct genetic effect or mate effect. Similary, the influence of the genotype of the dam is referred to as maternal-grandsire effect or indirect genetic effect. The mode of action of the direct genetic effect is supposed to be relatively simple: the sire transfers genes to the calf which are expressed in the calf phenotype (e.g. size, gestation length) which may affect the ease of birth. The maternal grandsire is supposed to act upon calving traits in a more complicated way. First, the maternal-grandsire effect contains a direct genetic component since the sire of the dam also transfers genes to the calf. This part of the maternal-grandsire effect is similar to the sire-of-calf effect but half of the size. Besides, the maternal grandsire may influence calving traits by transferring genes to the dam which actually find expression in the dam, for instance in the pelvic dimensions or by means of a maternal effect on the size of the calf. This is referred to as the maternal genetic component. The direct and maternal genetic component are suspected to interact. Estimates of relevant parameters are summarized in tables III to VI of chapter 1.
6. Difficulties are encountered in the genetic-statistical analysis of data on ease of calving and stillbirth because of their categorical nature. At least in theory, the non-normality, the location dependent variance and the non-additivity of effects involved reduce the value of the usual estimation and prediction techniques based on the linear model and on normality of traits.

In the sixties and seventies AI-organisations in the Netherlands gradually started to apply the results from the research on calving traits, those on the effect of parity and the sire-of-calf effect in particular, by introducing a so-called heifer-bull-programme. This involves the testing of young bulls for direct genetic effect on calving traits and the recommendation of low-risk bulls with respect to dystocia and stillbirth for heifer matings. At that time, the data collection procedure was not uniform over AI-organisations, whilst the method of sire evaluation was not optimized. At the end of the seventies the research project which underlies this thesis was started, with two main objectives:

1. Optimization of the heifer-bull-programme including data collection and sire evaluation.
2. Examination of alternative sire-selection strategies to reduce dystocia, with emphasis on the impact of maternal genetic effects and direct-maternal-interaction.

Sire evaluation for categorical traits

The optimization of data collection within the framework of the heifer-bull-programme is no subject-matter of this thesis, but one of the main results, a mark-sense card for birth recording which is used nation-wide now, is shown as figure 1 in chapter 4. In the optimization of sire evaluation, emphasis was laid on a comparison between the method of Best Linear Unbiased Prediction (BLUP), which has optimal properties with normally distributed data, and a pseudo-Bayesian nonlinear method of sire evaluation for categorical variates based on the "threshold" concept, when applied to binary and ordered tetrachotomous reponses.

Chapter 2 refers to a comparison of these two methods with simulated data with a family structure consisting of half-sib groups of equal or unequal size. Simulations were done at varying levels of heritability and incidences of the binary trait. The methods were compared for their ability to elicit responses to truncation selection. The nonlinear procedure, which is theoretically more appealing, proved to be superior in a mixed model setting when the responses were binary, the layout was highly unbalanced, heritability was moderate to high and the incidence was below 25%. When a one-way model was tenable or when responses were tetrachotomous, the results by both methods were very similar.

In a similar simulation study, it was examined whether the incorporation of heteroscedastic residual variance into the BLUP-model would improve the sire-ranking ability of this method with categorical variates (chapter 3). Such an "adjustment" was proposed in the literature. The results indicated however that the ability of BLUP to rank sires correctly for categorical traits is impaired by adjustments of this kind, particulary when responses are binary, in spite of a reduction in apparent prediction error variance. This is consistent with deductions from the theory of threshold models.

In a third study (chapter 4) BLUP, with homogeneous residual variance, and the nonlinear method were compared in estimating genetic merits for ease of calving and stillbirth under field conditions, i.e. with a data sample from the birth recording programme in the Netherlands. Since only minor differences in sire ranking were observed between the two methods, it is concluded that there is no clear advantage in applying the nonlinear prcedure, which entails more complicated and time consuming computations than BLUP, in sire evaluation for dystocia and stillbirth.

The results of these studies lead to the conclusion that BLUP with homogeneous residual variance, which is a standard method of sire evaluation for dairy traits in many countries, is fairly robust against the departures from normality and linearity arising with categorical data. Because of the computational expenses involved in the nonlinear procedure, particulary with large data sets, an appropriate BLUP-model which should at least correct for parity, sex of calf, herd and season of calving is advised for the evaluation of sires for dystocia and stillbirth in the Netherlands.

Sire selection for dystocia

Sire selection for direct genetic effect on dystocia may not be very appealin under the Dutch market conditions because dystocia is very highly correlated, in the genetic sense, with birth weight ($r_g \approx 0.9$) as shown in chapter 4. A reduction in level of dystocia by this type of selection would almost inevitably entail a reduction in birth weight which will lower the proceeds from the sale of young calves from the dairy farm. Since maternal effects are assumed to be involved in ease of birth, selection for traits contributing to maternal calving performance might be an alternative. With the exception of the pelvic inlet dimensions, which are difficult to measure and hence unsuitable for al large scale progeny test, such traits had not been identified. Chapter 5 refers to a study into the phenotypic association between ease of calving and a number of, mainly morphologic, dam traits in Holstein, Dutch Red and White and Dutch Friesian heifers. However, the only factor clearly associated with ease of calving was the size of the calf.

Since the attempt to identify dam traits with significant effect on calving performance failed, alternatives left apart from the heifer-bull-programme, are selection for direct genetic effect, with the disadvantage discussed, or selection for maternal-grandsire effect. Because of the suspected negative covariance between the direct and maternal genetic effects, it was felt necessary to examine the sign and the size of the covariance between the direct genetic effect and the maternal-grandsire effect. This necessity was underlined by a reluctancy among herdsmen to use the low-risk bulls identified in the heifer-bull-programme because they suspected that these bulls would sire small calves, which develop into small heifers and which run an increased risk of dystocia. In chapter 6 this hypothesis is examined in a two-way sire-selection trial with purebred Holstein, Dutch Red and White and Dutch Friesian cattle. Although the results were not entirely consistent over breeds, this study yielded additional evidence that direct and maternal-grandsire merits for ease of birth as well as for birth weight and gestation length are correlated positively. It was conjectured that the maternal-grandsire effect on ease of birth is dominated by direct inheritance of calf size. This conclusion implies that selection of sires for ease of birth of their progeny as calves is expected to yield a favourable response with respect to the ease of calving of their daughters and vice versa.

Selection programmes

In the final chapter, the monetary (discounted) returns from three schemes of breeding bull selection for calving traits (score for calving ease, birth weight, gestation length), viz. identification of low-risk bulls for heifer matings among breeding bulls selected for dairy traits, selection on direct genetic merit for calving traits in addition to selection for dairy traits and selection on maternal-grandsire merit for calving traits in addition to selection for dairy traits, are estimated for several calf price levels and incidences of dystocia. The first scheme, i.e. the heifer-bull-programme, proved to increase the returns from a breeding programme in dairy cattle, particularly when the incidence of dystocia or the calf price is high. Within such a scheme sire evaluation for birth weight and gestation length in addition to the evaluation for a score for calving ease contributes only marginally to the accuracy of low-risk-bull identification, at least when the latter is based on about 200 progeny per sire. Selection indices for direct genetic or maternal-grandsire effects on calving traits reduced the incidence of dystocia only at low calf prices (upto about Dfl 5.00 per kg). In the normal calf price range in the Netherlands (Dfl 7.50 - Dfl 15.00 per kg) either type of selection, if advisable at all, should be for an increase in birth weight in spite of a corresponding rise in incidence of dystocia. This is due to the highly positive genetic correlation between dystocia and birth weight. Because of a reduced intensity of selection for dairy traits, the impact of additional selection for birth weight on the total returns from the selection of breeding bulls in dairy cattle is either negative, or only marginally positive however. Consequently, the heifer-bull-programme is the most attractive breeding strategy to reduce dystocia.

SAMENVATTING

Het onderzoek naar de wetmatigheden van geboortemoeilijkheden en doodgeboorte bij rundvee kent reeds een historie van circa 20 jaar. De noodzaak van dit onderzoek wordt nog eens geïllustreerd door de percentages geboortemoeilijkheden en doodgeboorte die in het begin van de jaren '70 bij de belangrijkste Nederlandse runderrassen werden gevonden. Het percentage moeilijke geboorten bedroeg bij vaarzen 15 à 17% en bij de tweede-kalfs en oudere koeien 5 à 6%. Het percentage doodgeboorte lag bij deze kategorieën op respektievelijk 9 à 12% en 2,5 à 3,5%. Deze percentages zijn gebaseerd op KI-gegevens. In de zestiger en zeventiger jaren zijn vele wetenschappelijke publikaties over dit onderwerp verschenen. Deze betreffen verschillende aspekten van geboortemoeilijkheden en doodgeboorte, zoals frekwenties bij verschillende rassen en kruisingen, oorzaken, relaties met andere kenmerken, de schade die wordt veroorzaakt en faktoren die het vóórkomen mede bepalen. Hoofstuk 1 geeft een samenvatting van de resultaten van het onderzoek dat in genoemde decennia is verricht. Daaruit kunnen een aantal belangrijke konklusies worden getrokken die als uitgangspunten voor het onderhavige onderzoek mogen worden gezien. Deze konklusies zijn in de volgende punten samengevat.

1. Het optreden van doodgeboorte is in belangrijke mate toe te schrijven aan geboortemoeilijkheden: 40 à 60% van de gevallen van doodgeboorte in KI-gegevens treden op bij geboorten die als moeilijk worden gekwalificeerd. Daarnaast veroorzaken geboortemoeilijkheden schade vanwege de extra arbeid die van de veehouder wordt gevergd, de hogere dierenartskosten, een vermindering van de fertiliteit en van de melkproduktie van de betroffen koeien en het hogere percentage gedwongen afvoer.
2. Vaarzen en koeien (tweede kalfs en ouder) verschillen zowel in de mate van optreden als in oorzaak van geboortemoeilijkheden. Geboortemoeilijkheden treden bij vaarzen drie à vier keer zo frekwent op als bij koeien. Bij vaarzen is een (te) krappe verhouding tussen de omvang van het kalf en de ruimte in de geboorteweg van de moeder de belangrijkste oorzaak. Ook afwijkingen in de presentatie van het kalf geven veelvuldig aanleiding tot problemen. Bij koeien wordt het optreden van geboorteproblemen minder vaak toegeschreven aan de verhouding tussen de omvang van het kalf en de ruimte in de geboorteweg. Andere oorzaken, zoals zwakke weeën, een slag in de baarmoeder en onvoldoende ontsluiting zijn bij deze leeftijdskategorie relatief belangrijker.

3. Binnen genoemde leeftijdskategorieën neemt de kans op geboortemoeilijkheden toe met het gewicht en de afmetingen van het kalf bij de geboorte. Het fenotypische verband tussen deze kenmerken vertoont een drempelkarakter, d.w.z. de kans op geboortemoeilijkheden neemt plotseling sterk toe wanneer het formaat van het kalf een bepaalde drempelwaarde overschrijdt. De kans op geboortemoeilijkheden is eveneens positief gerelateerd aan de draagtijd. Waarschijnlijk is dit toe te schrijven aan een toename van het formaat van het kalf bij een langere draagtijd. Ook is er een verband aangetoond tussen de afmetingen van de bekkenopening van de koe en de kans op geboortemoeilijkheden, met name bij vaarzen.
4. Onder punt 2 is reeds gekonkludeerd dat de leeftijd (pariteit) van de koe een sterke invloed heeft op het vóórkomen van geboortemoeilijkheden. Andere faktoren met een duidelijke systematische invloed zijn het geslacht van het kalf en het seizoen van afkalven. Bij stierkalveren ligt de frekwentie over het algemeen twee maal zo hoog als bij vaarskalveren, hetgeen in overwegende mate is toe te schrijven aan het gemiddeld grotere formaat van stierkalveren. Verder blijkt de frekwentie van geboortemoeilijkheden in de landen van Noord-West Europa in de herfst en voorwinter meestal hoger te zijn dan in het voorjaar en de zomer. Een dergelijk seizoenspatroon, dat verband lijkt te houden met het houderijsysteem, wordt dikwijls ook gevonden ten aanzien van het geboortegewicht.
5. De kans op geboortemoeilijkheden en doodgeboorte wordt beïnvloed door het genotype van moeder en kalf. Dit geldt ook voor het geboortegewicht en de draagtijd. Vanwege de betrokkenheid van twee genotypes ontstaat een betrekkelijk komplex genetisch model. Met het oog op de selektie van stieren wordt de invloed van het genotype van het kalf dikwijls vadereffekt, direkt genetisch effekt of partnereffekt genoemd. Vanzelfsprekend ligt slechts de helft van de genetische aanleg van het kalf aan deze naamgeving ten grondslag. Om dezelfde reden wordt de invloed van het genotype van de koe aangeduid met moeders-vader-effekt of indirekt genetisch effekt. De wijze van expressie van het direkt genetisch effekt is in principe betrekkelijk eenvoudig: de vader van het kalf geeft genen door aan het kalf. Deze komen tot expressie in het phenotype van het kalf, bijvoorbeeld in formaat of draagtijd, en kunnen daardoor het geboorteverloop beïnvloeden. Het moeders-vader-effekt is meer komplex van aard. Ook de vader van de

koe geeft genen door aan het kalf die op dezelfde wijze tot expressie komen als besproken bij het direkt genetisch effekt. Dit wordt de direkt genetische komponent in het moeders-vader-effekt genoemd. De invloed van de vader van de koe langs deze weg is half zo groot als die van de vader van het kalf. Daarnaast kan de vader van de koe ook invloed hebben op het geboorteverloop via genen die in de koe tot expressie komen, bijvoorbeeld in de afmetingen van de bekkeningang of in de vorm van een maternaal effekt op het formaat van het kalf. Dit wordt de maternaal genetische komponent genoemd. Er zijn aanwijzingen voor een negatieve covariantie tussen de direkte en de maternaal genetische komponent. In de tabellen III tot en met VI van hoofdstuk 1 staan schattingen van de relevante genetische parameters vermeld.

6. Er doen zich problemen voor bij de genetisch-statistische analyse van gegevens over geboorteverloop en doodgeboorte omdat deze kategorisch van aard zijn. Omdat de genoemde kenmerken niet de normale verdeling volgen, de variantie nivo-afhankelijk is en de effekten niet-additief zijn, zijn de gebruikelijke schattingsmethoden die gebaseerd zijn op het lineaire model en op normaliteit van kenmerken minder geschikt, althans in theorie.

In de loop van de zestiger en zeventiger jaren begonnen de Nederlandse KI-organisaties de resultaten van het onderzoek naar geboortemoeilijkheden geleidelijk toe te passen in de vorm van het zogenaamde pinkenstierprogramma. Hierin worden proefstieren getest ten aanzien van hun direkt genetische invloed op geboortekenmerken. Stieren die weinig geboortemoeilijkheden en doodgeboorte blijken te veroorzaken worden aanbevolen voor pinken, waardoor de frekwentie bij de meest gevoelige leeftijdskategorie, de eerste-kalfs dieren, kan worden gereduceerd. Er bestonden evenwel verschillen tussen de KI-organisaties in de wijze van registratie van de kenmerken en in de methode van fokwaardeschatting, waardoor de term "aanbevolen voor pinken" niet eenduidig was. Aan het eind van de jaren zeventig werd het onderzoekprojekt, dat aan dit proefschrift ten grondslag ligt gestart, met als hoofddoelstellingen:

1. Optimalisatie van het pinkenstierprogramma, waaronder de wijze van registratie van kenmerken, de gegevensverzameling en de methode van fokwaardeschatting.
2. Onderzoek naar alternatieve methoden van selektie van stieren tegen geboortemoeilijkheden.

De verbetering van de wijze van registratie van kenmerken en van de gegevensverzameling valt buiten het kader van dit proefschrift. Eén van de belangrijkste resultaten daarvan, een optisch te lezen geboortergistratieformulier, dat momenteel op nationale schaal wordt gebruikt, is weergegeven als figuur 1 in hoofdstuk 4. In het onderzoek naar een optimale methode van fokwaardeschatting is de nadruk gelegd op een vergelijking van de methode die bekend staat als Best Linear Unbiased Prediction (BLUP) en die als beste methode wordt beschouwd bij normaal verdeelde kenmerken, met een pseudo-Bayesiaanse, niet-lineaire methode, ontworpen voor kategorische kenmerken, bij toepassing op binaire en geordende tetrachotome (in vier klassen ingedeelde) variabelen.

In hoofdstuk 2 worden deze twee methoden vergeleken met behulp van gesimuleerde datasets, waarvan de struktuur bestaat uit half-sib groepen van gelijke of ongelijke grootte. De vergelijking is uitgevoerd bij verschillende erfelijkheidsgraden en uiteenlopende frekwenties van het binaire kenmerk. De methoden zijn vergeleken op grond van de verkregen respons bij truncatie-selektie. De niet-lineaire methode, die op theoretische gronden meer aanspreekt, bleek betere resultaten te geven bij sterk ongebalanceerde, binaire data met een matige tot hoge erfelijkheidsgraad en een frekwentie van minder dan circa 25%, gegenereerd volgens een gemengd model. De verschillen tussen de methoden bleken verwaarloosbaar klein te zijn bij volgens een éénweg-model gegenereerde binaire data en bij tetrachotome data, ongeacht het model.

In een soortgelijke studie is nagegaan of de mogelijkheden van de BLUP-methode om stieren korrekt te rangschikken voor kategorische kenmerken zou kunnen worden verbeterd door in het model rekening te houden met heterogene restvariantie (hoofdstuk 3). Een dergelijke aanpassing is in de literatuur voorgesteld. De resultaten gaven aan dat dit averechts werkt, met name bij binaire gegevens.

In een derde studie (hoofdstuk 4) zijn de BLUP-methode, met homogene restvariantie, en de niet-lineaire methode vergeleken t.a.v. de fokwaardeschatting voor geboorteverloop en doodgeboorte onder "praktijkomstandigheden", met behulp van gegevens uit de Nederlandse geboorteregistratie. De methoden bleken slechts geringe verschillen te vertonen wat betreft de rangschikking van stieren voor deze kenmerken. Op grond daarvan is de konklusie getrokken dat de niet-lineaire methode van fokwaardeschatting, die aanmerkelijk gekompliceerder en tijdrovender is dan de BLUP-methode, geen duidelijke voordelen biedt bij de fokwaardeschatting voor geboortemoeilijkheden en doodgeboorte onder de huidige Nederlandse praktijkomstandigheden.

De resultaten van deze studies geven aan dat de BLUP-methode, die in diverse landen wordt toegepast bij de fokwaardeschatting voor melkproduktiekenmerken, betrekkelijk ongevoelig is voor de niet-normaliteit en niet-lineariteit zoals die zich bij kategorische kenmerken voordoen. Daarom wordt ten behoeve van de fokwaardeschatting voor geboorteverloop en doodgeboorte een BLUP-model acceptabel geacht, waarin tenminste moet worden gekorrigeerd voor pariteit, geslacht van het kalf, bedrijf en seizoen van afkalven.

Selektie van stieren voor geboortemoeilijkheden

Selektie van stieren op grond van hun direkt genetische invloed op geboortemoeilijkheden is waarschijnlijk niet erg aantrekkelijk in de Nederlandse marktsituatie, omdat dit vrijwel onvermijdelijk zou leiden tot een afname in geboortegewicht gezien de hoge genetische korrelatie tussen deze kenmerken ($r_g \simeq 0{,}9$; hoofdstuk 4). Daardoor zou de opbrengst uit de verkoop van nuchtere kalveren vanaf het melkveebedrijf teruglopen. Een alternatief zou zijn om te selekteren op kenmerken die de maternale invloed op het geboorteverloop bepalen. Met uitzondering van de afmetingen van de bekkeningang, die moeilijk meetbaar zijn en daarom ongeschikt moeten worden geacht voor een nakomelingenonderzoek op praktijkschaal, waren dergelijke kenmerken evenwel niet geïdentificeerd. Hoofdstuk 5 heeft betrekking op een onderzoek naar het fenotypische verband tussen het geboorteverloop en een aantal voornamelijk morfologische kenmerken van het moederdier bij Holstein-, MRY- en FH-vaarzen. De enige faktor die duidelijk verband hield met het verloop van de geboorte was evenwel het formaat van het kalf.

Aangezien de poging om aan het moederdier kenmerken met een wezenlijke invloed op het geboorteverloop vast te stellen mislukte, is niet duidelijk hoe op praktijkschaal op maternale invloed moet worden geselekteerd. Selektie op direkt genetische invloed, met het voornoemde nadeel, of selektie op moeders-vader-invloed zijn dan, afgezien van het pinkenstierprogramma, de overgebleven alternatieven. Vanwege een eventuele negatieve covariantie tussen de direkte en de maternale genetische invloed, werd het, voor een juiste schatting van de selektierespons, nodig geacht om het teken en de mate van de covariantie tussen het direkt genetische effekt en het moeders-vader-effekt vast te stellen. Deze noodzaak werd onderstreept door een zekere terughoudendheid bij de veehouders ten aanzien van het gebruik van pinkenstieren. Een veel gehoorde opvatting was dat de kleine kalveren die van deze stieren afstammen zich zouden ontwikkelen tot vaarzen van gering formaat met een verhoogde kans op geboortemoeilijkheden. Hoofdstuk 6 beschrijft de toetsing van deze hypothese door middel van een tweeweg-stieren-selektie-proef met raszuivere Holstein-, MRY- en FH-dieren. Hoewel de resultaten voor de drie rassen niet geheel overeenstemden, leverde dit onderzoek aanvullende bewijzen op dat de fokwaardes ten aanzien van de direkt genetische en de moeders-vader-invloed op het geboorteverloop positief gekorreleerd zijn. Ook voor geboortegewicht en draagtijd werd een positieve korrelatie gevonden. Dit houdt in dat dochters van stieren met weinig geboortemoeilijkheden bij hun nakomelingen als kalf relatief weinig problemen zullen hebben bij het afkalven, en omgekeerd.

Selektieprogramma's

In het laatste hoofdstuk worden drie programma's van fokstierselektie voor geboortekenmerken (geboorteverloop, geboortegewicht, draagtijd) vergeleken wat betreft gediskonteerde geldelijke opbrengsten. De programma's zijn:

1. het aanwijzen van pinkenstieren onder de op basis van melkproduktievererving geselekteerde fokstieren;
2. selektie op grond van direkt genetische invloed op geboortekenmerken in aanvulling op de selektie voor melkproduktievererving;
3. selektie op grond van moeders-vader-invloed op geboortekenmerken in aanvulling op de selektie voor melkproduktievererving.

De berekeningen zijn uitgevoerd voor verschillende prijsnivo's van nuchtere kalveren en bij verschillende uitgangsfrekwenties van geboortemoeilijkheden. Het pinkenstierprogramma bleek een gunstige invloed te hebben op de opbrengsten van het totale fokprogramma, vooral bij een hoge frekwentie van geboortemoeilijkheden bij vaarzen en/of hoge kalverprijzen. Ten behoeve van de selektie van pinkenstieren bleek het niet noodzakelijk te zijn om naast de fokwaardeschatting voor het geboorteverloop ook fokwaardes voor geboortegewicht en draagtijd te schatten. De laatstgenoemde fokwaardes bleken de nauwkeurigheid van pinkenstierselektie nauwelijks te verhogen, althans bij het in Nederland gebruikelijke aantal nakomelingen van ca. 200 per stier.

Index-selektie voor de direkt genetische of de moeders-vader invloed op geboortekenmerken leidde alleen tot een verlaging van het nivo van geboortemoeilijkheden bij lage kalverprijzen (tot ongeveer *ƒ* 5,00 per kg). Bij de voor Nederland normaal te noemen prijzen (*ƒ* 7,50 - *ƒ* 15,00 per kg) leidden beide vormen van selektie tot een verhoging van het nivo van geboortemoeilijkheden. Dit wordt veroorzaakt door de dan hoge ekonomische waarde van het geboortegewicht en de sterk positieve genetische korrelatie tussen geboortegewicht en geboortemoeilijkheden. Selektie van fokstieren voor geboortekenmerken zou evenwel de intensiteit van selektie op melkproduktievererving verlagen. De geldelijke opbrengsten van de selektie voor geboortekenmerken bleken niet of nauwelijks op te wegen tegen de afname van de opbrengsten uit de selektie op melkproduktievererving. Dientengevolge moet het pinkenstierprogramma worden beschouwd als de meest aantrekkelijke vorm van selektie om het nivo van geboortemoeilijkheden te verlagen.

Curriculum Vitae

Albert Meijering werd op 24 november 1951 geboren te Stieltjeskanaal, gemeente Dalen (Drente), waar hij ook het lager onderwijs volgde. Na het behalen van het gymnasium-bèta-diploma aan het Coevorder Lyceum te Coevorden in 1970 begon hij, in september van dat jaar, met zijn studie aan de Landbouwhogeschool te Wageningen. Het doctoraalexamen in de Zoötechniek, met als hoofdvakken de Gezondheids- en Ziekteleer der Huisdieren en de Fysiologie van de Huisdieren en als bijvak de Veevoeding, werd afgelegd in januari 1976. In december 1975 trad hij in dienst van het Ministerie van Landbouw en Visserij als wetenschappelijk medewerker bij het Instituut voor Pluimvee-onderzoek "Het Spelderholt" te Beekbergen met als taak het onderzoek op het gebied van de voeding van legpuimvee. Van oktober 1977 tot december 1985 was hij als wetenschappelijk medewerker, belast met het onderzoek op het terrein van de geboortemoeilijkheden bij runderen en later van de rundveefokkerij in het algemeen, verbonden aan het Instituut voor Veeteeltkundig Onderzoek "Schoonoord" te Zeist. Vanaf januari 1986 vervult hij de funktie van Consulent in Algemene Dienst voor de Rundveeverbetering bij het gelijknamige consulentschap te Arnhem.