Genetic aspects of
intervals from weaning to estrus
in swine

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Genetic aspects of intervals from weaning to estrus in swine

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Proefschrift
ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit te Wageningen
dr. C.M. Karssen,
in het openbaar te verdedigen
op 11 oktober 1996
des namiddags te één uur dertig in de Aula.

This thesis was compiled at:
Research Institute for Animal Science and Health (ID-DLO)
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Omslagontwerp met medewerking van Michiel, Rianne, Seref, Antigonnie, Jan en Wilco.

CIP-DATA KONINKLIJKE BIBLIOTHEEK, DEN HAAG
ISBN 90-5485-600-9

Ten Napel, J., 1996. Genetic aspects of interval from weaning to estrus in swine (Genetische aspecten van het interval spenen-bronst bij varkens). Genetic variation in interval from weaning to estrus, and genetic relationships with traits commonly under selection were studied using data from an eight-generation selection experiment on a short interval from weaning to estrus, and data from an American breeding company. From the biological background and the distribution of data it appears that interval from weaning to estrus is either normal or prolonged. Selection for a short interval reduced the average interval by reducing the incidence of prolonged intervals only. Sows on units of the breeding company studied with a prolonged interval had consistently more favorable estimated breeding values for backfat and growth rate, than sows with a normal interval. Analysis of data from the selection experiment did not confirm this. Model studies showed that extending the number of traits under selection with a 0/1 trait, representing normal and prolonged intervals, gives the highest response in each of the traits under selection. *Thesis, Department of Animal Breeding, Wageningen Agricultural University.*

Stellingen

1. Het aantal dagen tussen het afspenen van de biggen en de eerste bronst (interval spenen-bronst) na de eerste worp is vanuit biologisch oogpunt gezien een ander kenmerk dan interval spenen-bronst na latere worpen.
Dit proefschrift

2. Variatie in interval spenen-bronst wordt veroorzaakt door variatie in het optreden van stille bronst, variatie in het vóórkomen van een verlengd interval en variatie in de lengte van normale en verlengde intervallen.
Dit proefschrift

3. Verschillen tussen fokprogrammas en verschillen in bedrijfsvoering hebben nauwelijks invloed op de gemiddelde lengte van normale en verlengde intervallen spenen-bronst, maar veroorzaken wel variatie in het vóórkomen van verlengde intervallen.
Dit proefschrift

4. Genetische selectie voor economisch belangrijke kenmerken, zoals rugspek, groei per dag en worpgrootte, kan een verlenging van het gemiddelde interval spenen-bronst tot gevolg hebben, veroorzaakt door een toename van het aantal verlengde intervallen als gecorreleerde respons van selectie.
Dit proefschrift

5. Het feit dat een lang interval spenen-bronst een breed scala van mogelijke oorzaken heeft, maakt het bijzonder moeilijk om zulke verbanden die oorzakelijk zijn aan te tonen.
Dit proefschrift

6. Het concept van een verdeling die bestaat uit een verdeling van normale waarnemingen en een verdeling van waarnemingen veroorzaakt door een probleemsituatie kan mogelijk ook worden toegepast op het celgetal bij melkkoeien.

7. Als de expressie van een kwantitatief kenmerk te beschouwen is als één of meer ketens van processen, dan verklaart een *Quantitative Trait Locus* (QTL) alleen variatie in de expressie van dat kenmerk bij die dieren waar het proces waarop het QTL-produkt invloed heeft de beperkende factor in de keten is; in zijn algemeenheid zal dit slechts voor een deel van de dieren in de populatie het geval zijn.

8. Fysiologie van genetische variatie zou een integraal onderdeel moeten zijn van associatiestudies, om de gevolgen van selectie ten gunste van individuele allelen te bestuderen.

9. Een wetenschappelijk onderzoeker kan als geen ander onderscheiden in hoeverre conclusies van haar/zijn onderzoek berusten op feiten, interpretatie of paradigma, en mag zich derhalve niet onttrekken aan de informatievoorziening ten behoeve van politieke besluitvorming.

10. De huidige praktijk op middelbare scholen dat natuurwetenschappelijke modellen niet als model maar als werkelijkheid gedoceerd worden werkt overschatting van wetenschap en techniek in de samenleving in de hand.

11. De belangrijkste oorzaak van het wachtgeld-probleem van universiteiten, veroorzaakt door AIO's, is het opleiden van een structureel veel groter aantal wetenschappelijk onderzoekers dan wordt gevraagd op de arbeidsmarkt.

12. Eigenwijsheid is noodzakelijk voor vernieuwing, maar voor iemand met deze eigenschap leidt het hoofdzakelijk tot frustraties.

13. Je concentratievermogen is meestal een dag eerder en een dag langer op vakantie dan jezelf.

J. ten Napel
Genetic aspects of intervals from weaning to estrus in swine
Wageningen, 11 oktober 1996

Voorwoord

De liefde voor de veehouderij heb ik opgedaan tijdens vakanties en op vrije zaterdagen. Vanaf dat ik een jaar of vijftien was, ging ik vaak helpen op het bedrijf van Kees Jan en Jannie van Loo, en op het bedrijf van oom Klaas en tante Fenny. Na het VWO had ik het idee dat ik te weinig koeien en varkens zou zien als ik naar de LU zou gaan, en koos daarom voor de Agrarische Hogeschool in Dronten. De halfjaarsstage heb ik op 't Gen gedaan, bij Kor Oldenbroek. Ik geloof dat deze stage cruciaal is geweest voor mij. Ik vond het geweldig om onderzoek te doen. Gestimuleerd door Kor ben ik daarom na de militaire dienst 'doorgestroomd' naar de LU, met het doel om assistent in opleiding (AIO) te worden. Achteraf gezien denk ik dat ik inderdaad vrij weinig koeien en varkens had gezien als ik direct naar de LU was gegaan. In eerste instantie leek het erop dat er geen vacature voor een AIO zou zijn, maar onverwacht was er toch één bij het IVO-DLO in Zeist.

Ik kijk nu terug op vier jaar AIO. Ik zou die periode als volgt kunnen typeren. Het is te vergelijken met een wandelvakantie van vier weken, waarbij het in de tweede helft van de eerste week begint te regenen, terwijl je paraplu lekt, maar waarbij het in de tweede helft van de derde week toch nog opklaart, zodat je bij thuiskomst aan iedereen vertelt dat je een goede vakantie hebt gehad.

De samenstelling van mijn begeleidingsgroep is nogal veranderd in de loop van de tijd. Toch geloof ik niet dat dat sterk bijgedragen heeft aan de lekkende paraplu. Bas Kemp, Ella Luiting, Joop te Brake, Tette van der Lende, Julius van der Werf, Kor Oldenbroek, bedankt voor het meedenken en kritisch commentaar geven op mijn wilde ideeën. Alfred de Vries en Theo Meuwissen, bedankt voor de meer intensieve begeleiding. Hoewel we geregeld van mening verschilden, is het toch zeer essentieel gebleken voor dit proefschrift. Pim Brascamp, bedankt voor je support op momenten dat ik dacht dat de hele wereld mijn ideeën maar onzin vond.

My stay at the University of Nebraska in Lincoln put me back on track after a difficult period. Rodger Johnson, you were not sure which way to go, either, but you motivated and supported me, and you were as much interested in the results as I was. Thank you very much for your help. Curt van Tassell, you have no idea how important it turned out to be for me that I shared the appartment with you. You were a very nice colleague, and you've been a great friend.

Ik heb in de vier jaar als AIO veel aardige mensen ontmoet, die in meer of mindere mate (of soms zelfs helemaal niet) hebben bijgedragen aan mijn werk. Je zou kunnen zeggen dat deze mensen samen veroorzaakten dat het prettig werken was op het IVO. Een paar namen wil ik noemen:

Henriëtte, Ronald, Nicoline, Truus, Albert. Astrid.

De belangrijkste ontmoeting van de afgelopen vier jaar was wel toen ik Anneke tegenkwam. Waar een verregend weekend op Schiermonnikoog al niet goed voor is... Anneke, het is fijn bij jou, en ik beloof dat ik niet meer 's morgens zal gaan werken, als je weer op zaterdag je verjaardag viert. En van één ding mag je zeker zijn: You've got a friend.

Het idee dat objectief onderzoek mogelijk zou zijn is een hardnekkige misvatting. Elke onderzoeker neemt waar door een bril die gekleurd is door zijn of haar levensvisie. Ik leg hierbij verantwoording af voor de (in de wetenschap misschien niet zo gangbare) kleur van mijn bril. Net zoals andere wetenschappers (zouden moeten) doen, houd ik me bezig met vragen omtrent 'struktuur' en 'functioneren'. Mijn levensvisie is richtinggevend: het geeft antwoord op vragen omtrent oorsprong en bestemming of bedoeling. Dit soort vragen zijn niet wetenschappelijk te beantwoorden. Ik geloof in een wereld die geschapen is door God. Hij houdt zich nog steeds actief bezig met die wereld. Concreet voor mijn werk betekent dat dat een varken geschapen is om te functioneren als een geheel. "En God zag dat het goed was." Fysiologische mechanismen in een varken zijn niet "toevallig zo ontstaan", maar ontworpen. Er zit een bedoeling achter. De consequentie van een bijbelse levensvisie is ook dat niet ons menselijk waarnemings- en bevattingsvermogen uiteindelijk norm is, bijvoorbeeld bij theorievorming, maar Gods Woord. Verder betekent het voor mijn werk dat ook dat aspect van mijn leven door God wordt geleid, zoals Hij het leven van iedereen leidt, of je je daar nu van bewust bent of niet. En dus past het mij ook om Hem te bedanken voor het feit dat mijn proefschrift nu af is.

Jan

CONTENTS

Samenvatting

De moderne varkenshouderij stelt hoge eisen aan een varken.[1] Dat komt omdat varkenshouders zo efficiënt mogelijk willen produceren. Ze proberen de efficiëntie te verhogen door de bedrijfsvoering te verbeteren (voer, huisvesting) en door middel van fokkerij. Een vleesvarken dat in biologische en economische zin efficiënt is, groeit in een zo kort mogelijke tijd naar het gewicht waarop het geslacht kan worden. Het varken mag bij dat gewicht niet teveel rugspek hebben, omdat de consument dat niet wil en omdat het veel voer kost. Het is belangrijk vanuit economisch oogpunt dat het varken niet teveel voer verbruikt heeft tijdens de groei. Een efficiënte fokzeug (moederdier) brengt een zo groot mogelijk aantal biggen per jaar groot. Om kans van overleven van de biggen zo groot mogelijk te maken is het belangrijk dat de zeug voldoende melk geeft. Het fokbeleid is er daarom meestal op gericht om elk van deze kenmerken te verbeteren.

Een zeug heeft van nature in de zoogperiode een hoge melkgift per dag: het gewicht van een toom van tien tot twaalf biggen kan in de eerste vier weken toenemen tot meer dan vier keer het geboortegewicht. Vooral in de eerste anderhalve week is de melkgift is al hoog, maar blijft de eetlust nog achter. Veel zeugen verliezen daarom gewicht in deze periode. Dit verschijnsel zie je zowel in de intensieve varkenshouderij, als bij het wild zwijn.

Van nature zijn zeugen dan ook alleen bij uitzondering vruchtbaar in de zoogperiode. De prioriteit ligt bij de pasgeboren biggen, en niet bij een mogelijk nieuwe dracht. De bronstcyclus komt meestal niet eerder op gang dan dat de biggen niet meer drinken bij de moeder. Het bij de moeder weghalen wordt spenen of afspenen genoemd. Normaal gesproken treedt de eerste bronst dan na een dag of vier op.

Door het streven naar efficiënte vlees- en fokvarkens neemt de belasting van zeugen in de zoogperiode toe. Selectie gericht op efficiënte vleesvarkens heeft soms als bijverschijnsel dat de eetlust iedere generatie een beetje minder wordt. Ook lichaamsreserves in de vorm van rugspek worden iedere generatie minder. Selectie voor efficiënte fokzeugen vergroot de

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[1] *Deze samenvatting is bedoeld voor een breed publiek. In de engelstalige samenvatting wordt dieper ingegaan op de wetenschappelijke kant van de resultaten.*

inspanning die de zeug moet leveren, als de melkgift en het aantal biggen toeneemt. Een zeug van een dergelijke foklijn moet dus eigenlijk méér doen met minder middelen. Vooral jonge zeugen, die zelf nog groeien, komen hierdoor in de problemen. Ze hebben meer behoefte aan voer dan ze op kunnen. Ze verliezen gewicht, terwijl ze toch over voldoende voer beschikken.

Net zoals bij de meeste zoogdieren heeft een tekort aan lichaamsreserves ook bij varkens tot gevolg dat de vruchtbaarheid tijdelijk minder wordt, tot lichaamsreserves weer aangevuld zijn. Bij vrouwelijke dieren stopt de cyclus tijdelijk. Om precies dezelfde reden hebben topatletes nogal eens problemen met de menstruatie. Bij zeugen die ernstig tekort komen in de zoogperiode komt de cyclus niet direct op gang na het afspenen van de biggen, maar pas na verloop van tijd.

Er zijn nog meer oorzaken mogelijk voor het niet op gang komen van de cyclus. Soms toont een zeug de bronst niet, en dan lijkt het alleen of de bronst niet op gang komt. Dit wordt stille bronst genoemd. Stress vlak voor en tijdens de bronst, bijvoorbeeld veroorzaakt door hergroeperen, is een belangrijke oorzaak van het niet laten zien van bronst. Als stress langer duurt kan het ook de cyclus ontregelen. In dat geval kan het heel lang duren voor de cyclus weer normaal is. Van nature beïnvloedt ook de daglengte het op gang komen van de cyclus.

Uit onderzoeken blijkt dat op een groot deel van de Nederlandse bedrijven een derde tot de helft van de jonge zeugen na het grootbrengen van de eerste worp niet op het normale tijdstip bronstig wordt. Een deel van deze zeugen wordt met een hormoonbehandeling kunstmatig in cyclus gebracht. Op bedrijven waar men dat niet toepast worden zeugen afgevoerd als ze niet binnen een bepaalde tijd bronstig zijn. Zowel uit economisch oogpunt, als uit het oogpunt van de gezondheid en het welzijn van de zeug is het dus van belang om het vóórkomen van het niet-normaal op gang komen van de cyclus tegen te gaan.

In dit proefschrift staan eigenlijk twee vragen centraal. De eerste vraag is of het normaal op gang komen van de cyclus erfelijk bepaald is. De tweede vraag is of er een aantoonbaar verband is met het streven naar efficiënte vlees- en fokvarkens. Verder is er een korte studie gedaan naar de mogelijkheden om wat te doen aan dit probleem.

Varkenshouders drukken het op gang komen van de cyclus uit in het aantal dagen tussen het afspenen van de biggen en de eerste bronst. Dit wordt interval spenen-bronst genoemd. Om te kijken of dit kenmerk verbeterd kan worden met fokkerij, is in de jaren tachtig op het

IVO-DLO in Zeist een experiment uitgevoerd. Acht generaties lang zijn alleen dieren geselecteerd van moeders met een kort interval spenen-bronst (selectielijn). In een tweede lijn werd niet geselecteerd (controlelijn). Na afloop bleek inderdaad dat interval spenen-bronst erfelijk bepaald is, en dat selectie effectief was. Verder bleek uit de frequentie van waargenomen intervallen dat er inderdaad onderscheid is tussen normale intervallen (cyclus komt normaal op gang) en verlengde intervallen (cyclus komt niet normaal, maar pas later op gang). De selectie had niet tot gevolg dat stille bronst minder vaak voorkwam.

De tweede vraag kan eigenlijk op twee manieren bestudeerd worden. Eén manier is om te kijken hoe het aantal normale intervallen verandert onder invloed van selectie op kenmerken die de efficiëntie van vlees- en fokvarkens bepalen. Analyse van gegevens van twee bedrijven van een Amerikaanse fokkerijinstelling liet zien dat zeugen met een verlengd interval gemiddeld een gunstiger fokwaarde hadden voor elk van de kenmerken waarop werd geselecteerd, dan zeugen met een normaal interval spenen-bronst. Het beeld was hetzelfde op beide bedrijven.

De andere manier is om te kijken hoe de efficiëntie-kenmerken veranderen als gevolg van de selectie voor een kort interval spenen-bronst. Na afloop van het selectie-experiment op het IVO-DLO was niet één van de efficiëntie-kenmerken wezenlijk verschillend tussen de selectielijn en de controlelijn. Eigenschappen gemeten tijdens de opfok waren niet gerelateerd aan het optreden van verlengde intervallen. Sommige kenmerken gemeten in de zoogperiode (aan de zeug of de biggen) lieten wel een verband zien.

Omdat er zo veel mogelijke oorzaken zijn voor een verlengd interval, is het erg moeilijk om met de tweede manier een bestaand verband ook echt aan te tonen. Varkensfokkers moeten er echter wel rekening mee houden dat selectie voor efficiënte vlees- en fokvarkens een toename van verlengde intervallen spenen-bronst kan veroorzaken.

Selectie tegen verlengde intervallen is niet eenvoudig. Als een varkensfokker dat wil doen, kan hij het beste normale intervallen spenen-bronst (zeven dagen of korter) coderen met een 0, en verlengde intervallen (langer dan zeven dagen) met een 1. Met behulp van speciale programmatuur kunnen dan fokwaardes geschat worden voor het optreden van een verlengd interval. Op deze fokwaardes kan hij dan de selectie baseren.

De conclusie van dit proefschrift is dat het optreden van een verlengd interval spenen-bronst erfelijk bepaald is, en dat genetische verbanden met kenmerken die de efficiëntie van vlees- en fokvarkens bepalen weliswaar moeilijk aantoonbaar zijn, maar zeker niet onderschat moeten worden. Gecombineerde selectie op efficiëntie van vleesvarkens en normale intervallen kan dit probleem voor een groot deel ondervangen.

Chapter 1

General introduction

Jan ten Napel

The majority of sows that are suckling a litter, does not ovulate and show estrus, until the litter is weaned. There is, however, an enormous variation in the time from weaning to showing estrus, especially in first-litter sows.

When Burger (1952) reviewed the scientific literature of his days, he did not find an effect of parity on the length of the interval from weaning to estrus. In the late sixties and seventies, after modern pig breeding programs had been introduced, it became clear that problems with rebreeding sows after weaning were more pronounced in first-litter sows, than in older sows (Elsley et al., 1969; Maclean, 1969; Aumaitre et al., 1976). Although the entire pig production system changed drastically in this period (e.g. pigs were kept indoors, suckling period was reduced from seven or eight weeks to three weeks or less), it may have been one of the first indications that selection for improved production affected rebreeding performance of young sows. Initially, most research focused on effects of management on rebreeding sows, such as the amount and quality of diets fed during lactation and after weaning, type of housing, season, social environment (e.g. introduction of boars), relocation, etc. Except for the paper of Dyck (1971), showing between-breed variation, no attention was paid to genetic variation until the paper of Fahmy et al. (1979) was published. Afterwards, a few studies reported heritabilities for the farrowing interval (Johansson, 1981; Johansson and Kennedy, 1985; Maurer et al., 1985), which includes the interval from weaning to estrus. In general, genetic variation in the interval from weaning to estrus was considered unimportant, compared to variation due to management (Fahmy, 1981).

It has been estimated that between a third and a half of all first-litter sows on Dutch commercial herds is not seen in estrus in the first week after weaning. On commercial weaner-producing herds, these sows are usually treated with hormones to induce estrus, or otherwise culled because of anestrus. Because hormonal treatment is an easy, effective, and relatively inexpensive way to avoid long intervals from weaning to estrus, poor rebreeding performance is generally not regarded as a real problem. However, in sustainable pig production systems, routinely treatment with exogenous hormones to induce estrus is not acceptable. Furthermore, poor rebreeding performance is in many cases a problem of metabolic imbalance, which is not acceptable as a structural phenomenon either. Sustainable pig production systems involve healthy animals, which do not need more veterinary assistance as strictly necessary, which are able to produce without stimulating agents, and which are able to cope with permanent and temporary changes in their environment. So we should try to improve the level of management and, if possible, decrease the genetic liability for poor rebreeding performance.

The aim of this thesis is to study whether the interval from weaning to estrus of young sows has a genetic basis, whether poor rebreeding performance is related to economically important traits currently under selection, and whether it is possible to reduce the genetic liability for poor rebreeding performance.

Interval from weaning to estrus is a very complex trait. Estrus is the result of a cascade of processes leading to proper development of follicles, which can be disturbed in many ways. Apart from this, if the first estrus is not observed, the next estrus will not occur until an estrous cycle is completed. Chapter 2 describes the biology of the trait, and it is discussed which of the traits that contribute to variation in interval from weaning to estrus may have a genetic component. There is evidence for a distinction between normal and prolonged intervals, and it is discussed how in modern pig breeding schemes the genetic liability for a prolonged interval may increase.

Estimation of genetic variation in a trait requires a set of non-censored data, which is usually not available for interval from weaning to estrus on commercial herds, due to culling. For this reason no culling was applied in a selection experiment for a short interval from weaning to estrus. Genetic variation, efficacy of selection, and changes in the distribution of observed intervals due to selection in this experiment are described in Chapter 3. Data from this experiment are also used to test the concept of normal and prolonged intervals.

There are several ways to estimate relationships between traits. Apart from designing an experiment to estimate the relationships, sets of data obtained from practice can be analysed as well. Data from populations of a commercial breeding company, selected on an index of estimated breeding values for backfat and average daily gain, were used to study the genetic relationships between the traits under selection and incidence of prolonged intervals. Although intervals from weaning to estrus are not observed on sows that are culled because of anestrus, it is clear that the interval would have been prolonged, so records on culled sows can be included when estimating a genetic relationship between a continuous trait and incidence of prolonged intervals. This analysis is described in Chapter 4. Estimation of a genetic correlation with a binary trait is not straightforward, so genetic relationships are estimated by calculating the difference in estimated breeding value for the continuous trait between sows with a normal and sows with a prolonged interval.

A similar approach was followed when studying the correlated responses of selection for a short interval from weaning to estrus. In addition, genetic correlations with the length of normal intervals and with the length of prolonged intervals were estimated. Correlated responses in breeding traits are described in Chapter 5; those in rearing traits in Chapter 6.

Alternative strategies to select against prolonged intervals were compared by simulating a 120-sow nucleus herd with 10 generations of selection. In this study the concept of normal and prolonged intervals was used to simulate intervals from weaning to estrus. Genetic parameters were obtained from Chapter 5 and 6. The simulation model and the results of the comparison are described in Chapter 7.

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Chapter 2

A biological approach to examine genetic variation in weaning-to-oestrus interval in first-litter sows: a review

Jan ten Napel
Bas Kemp
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Alfred de Vries

Published in Livestock Production Science 41 (1995) 81

Abstract

To study genetic variation in weaning-to-oestrus interval, a model has been developed dividing the trait into the interval from weaning to the start of cyclic activity (IWSC), the interval between start of cyclic activity and oestrus (ISCO), the incidence of silent oestrus (SO) and the length of the oestrous cycle (CL). ISCO and CL appear to vary little, and therefore their contribution to genetic variation is likely to be negligible. Because there is no evidence in literature for genetic variation in SO, it is concluded that genetic variation in the weaning-to-oestrus interval is mainly due to genetic variation in IWSC. It is hypothesized that the nature of genetic variation in IWSC is the ability of sows to respond to appropriate stimuli, like boar contact. Severe losses of body weight, seasonal effects and stressors are known to be able to suppress this ability. Genetic selection for production and reproduction traits may limit feed intake capacity, reduce body reserves at first parturition, decrease rate of maturity at first parturition, and increase milk production capacity. These effects may increase the probability of severe losses of body weight during first lactation and subsequently a prolonged weaning-to-oestrus interval.

Key words: Sows; Postweaning oestrus; Genetic variation; Reproduction

Introduction

In normal conditions, sows are expected to return to oestrus within about one week after weaning. A longer period of anoestrus after weaning is often found to be associated with metabolic imbalance, disease or stress. Nevertheless, it is common practice to induce oestrus with exogenous hormones when sows do not return to oestrus within two or three weeks. Thus, not only for economical reasons, but also for reasons of animal health and welfare, it is desirable to reduce incidence of delayed oestrus after weaning. Generally, a delayed oestrus after weaning is mainly a problem in sows after their first litter and to a lesser extent in second-litter sows. The present paper is focused on the first parity.

Many factors are reported to influence the onset of the oestrous cycle, but relatively little attention has been paid to genetic variation. Between-breed variation in the weaning-to-oestrus interval was found to be considerable (Maclean, 1969; Aumaitre et al., 1976; Maurer et al., 1985). Few estimates of heritability from direct analyses of the interval between weaning and oestrus exist, ranging from .14 to .36 (Fahmy et al., 1979; Molenaar and Van der Steen, 1983; Petrovicová et al., 1988; Ten Napel et al., 1992). These are rather high, compared to other traits concerning fertility. Phenotypic variance is more often reported and large differences between estimates exist. Furthermore, sows in nucleus breeding herds not in oestrus within two to four weeks, are commonly culled. Both this culling practice and treatment with hormones on commercial herds yield a truncated distribution and cause additional variation between estimates. Consequently, estimates of parameters of the weaning-to-oestrus interval are difficult to interpret and may be of very limited value. It is clear that genetic parameters are desired, which have a general value for a range of breeds and environments. Therefore, an alternative approach is proposed in the present paper, based on biological knowledge.

The aims of this paper are (1) to review factors influencing underlying components of the interval between weaning and first detected oestrus in first-litter sows, and (2) to discuss in which components genetic variation is apparent.

Oestrus and follicular growth

Oestrus involves the characteristic symptoms and behaviour of a sow associated with ovulation and sexual receptivity. Main characteristics are reddening and swelling of the vulva, and showing the standing reflex (Willemse and Boender, 1966). Normally, oestrus is not exhibited until follicles have reached preovulatory size.

Development of follicles can be separated into two phases: a gonadotrophin-independent and a gonadotrophin-dependent phase. Development of primordial follicles into antral stage continues during all reproductive stages, like pregnancy and lactation, and is controlled by intraovarian factors. Although metabolic state may influence this process, it is in essence an autonomic process. This continuous development results in a permanent pool of antral follicles (Britt et al., 1985).

Luteinizing hormone (LH), which is under hypothalamic control by means of gonadotrophin-releasing hormone (GnRH), is released by the pituitary gland in a pulsatile pattern. A high-frequency-low-amplitude LH pattern is thought to be the major factor in the weaned sow permitting antral follicles to escape from atresia and to grow to preovulatory size (Kraeling and Barb, 1990). Hunter and Wiesak (1990) suggest that this recruitment takes place between d 14 and 16 of the oestrous cycle.

Induced by LH, antral follicles start producing androgens from progesterone produced within the follicle. The synthesis of oestrogen from androgens is stimulated by FSH (see reviews of Britt et al., 1985; Ainsworth et al., 1990). Whether a follicle is recruited or becomes atretic, depends on successful initiation of this oestrogen production in the follicle (Foxcroft and Hunter, 1985).

Oestrogen concentrations increase in recruited follicles and at a threshold level a positive feedback response of LH to oestrogen arises, which causes the preovulatory LH surge. After the initial rise in plasma LH, plasma oestrogen concentrations decline rapidly. The high levels of oestrogen stimulate oestrous behaviour. The preovulatory LH surge initiates processes which lead to ovulation. Nevertheless, both oestrus without ovulation (Eliasson, 1989) and ovulation without oestrus (Paredis, 1962) occur.

During pregnancy and lactation, the pulsatile LH release and later stages of follicular development are suppressed. Antral follicles become atretic and are replaced by smaller antral follicles in the pool. High plasma progesterone concentrations cause suppression during pregnancy. During lactation, the suckling stimulus is thought to be responsible for decreased pulsatile GnRH release from the hypothalamus (Foxcroft, 1992). A gradual increase in pulsatile LH secretion with increasing frequency and decreasing amplitude is observed during lactation in sows which return to oestrus four to six days after weaning (Shaw and Foxcroft, 1985; Tokach et al., 1992). This is attributed to a decreasing inhibition by suckling. The increasing pulsatile LH release causes a gradual shift in numbers of normal and atretic follicles

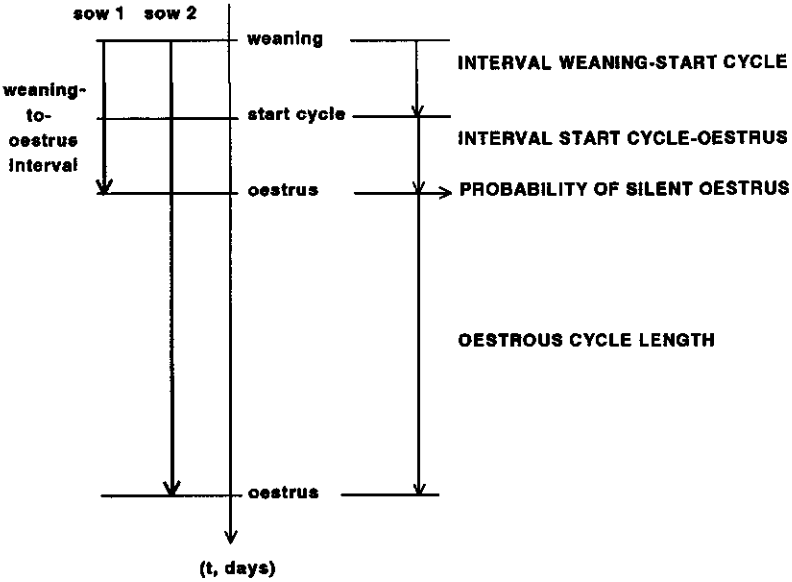

Figure 1. Components of the weaning-to-oestrus interval in case of a detected (sow 1) and a silent oestrus (sow 2).

from 1-to-2 and 2-to-3 mm classes towards 3-to-4 and 4-to-5 mm classes (Kunavongkrit et al., 1982).

At weaning, inhibition by suckling disappears, which results in a sudden elevation of GnRH and LH levels and an increased frequency of pulses (Shaw and Foxcroft, 1985). Sows which will not ovulate and remain anoestrous for some time after weaning, are lacking the pattern of increasing pulsatile release of LH (Tokach et al., 1992).

Biology of variation in weaning-to-oestrus interval

Components

Because oestrus is not the first step in the process involved in the onset of the oestrous cycle, weaning-to-oestrus interval can be divided in the time between weaning and start of cycle, and the time between start of cycle and oestrus. However, first observed oestrus is not always oestrus at first ovulation, for sows sometimes fail to exhibit oestrous behaviour, although they ovulate (Burger, 1952; Paredis, 1962). In case of a silent oestrus, sows will not return to oestrus before the current oestrous cycle is completed. Components of the weaning-to-oestrus interval in case of a detected (sow 1) and a silent oestrus (sow 2) are shown in Figure 1. Written as a model, we get:

Weaning-to-oestrus interval = Interval weaning to start of cycle + Interval start of cycle to detected or undetected first oestrus + SO * Oestrous cycle length,

where SO (0, 1, 2, 3, ...) indicates the occurrence of silent oestrus.

Factors reported to influence weaning-to-oestrus interval may impact on the different components. The literature concerning the influence of these factors does not generally distinguish these components. Nevertheless, based on hormonal data, we have attempted to establish for each of the various factors, the component on which they act. Because most factors appear to impact on 'Interval weaning to start of cycle', we will start discussing the other three components.

Interval from start of cycle to detected or undetected first oestrus

The start of the cycle can be considered to commence when re-initiation of the processes leading to ovulation occurs, whether or not ovulation is accompanied by sexual receptivity. We consider recruitment of follicles from the proliferating pool to be the start of cyclic activity, because it is the first step in the development of antral follicles to ovulatory size.

A specific LH pattern is thought to be the appropriate stimulus for recruitment of follicles in the weaned sow. Britt et al. (1985) summarized six trials, in which GnRH was administered every hour or every two hours to lactating sows. The time from start of treatment to oestrus varied from 84 to 128 h, or 3.5 to 5.3 d. Because of this relatively small range, we conclude that the contribution of variation in this component to the variation in the weaning-to-oestrus interval is of minor importance.

Table 1. Proportion of sows that experienced silent oestrus postweaning

	PAR[a]	N[a]	NNO[a]		NSO[a]	DAY [a]	EFFECTS ON INCIDENCE OF SILENT OESTRUS	
Dyck, 1972	m	120	28	(16d)	1	16	no effect of breed (Yorkshire vs. Lacombe)	
Reese et al., 1982a	p	191	24	(15d)	3	15	no effect of feeding 33.5, 50.2 or 67.0 MJ ME/d during lactation (sum of three experiments)	
Reese et al., 1982b	m	44	6	(15d)	0	15	no effect of feeding 33.5 or 67.0 MJ ME/d during lactation	
Cox et al., 1983	p	62	14	(14d)	10	14	no effect of supplementing 10% fat to lactational diet or weaning procedure	
King and Williams, 1984a	p	80	28	(21d)	11	18	no effect of lactational or postweaning food intake	
King and Williams 1984b	p	68	8	(8d)	1	18	no effect of energy or crude protein intake	
Nelssen et al., 1985	p	146	12	(15d)	1	15	no effect of feeding 41.9, 50.2 or 58.6 MJ ME/d during lactation	
King and Dunkin, 1986	p	72	35	(8d)	1	14	no effect of lactational food intake	
Johnston et al., 1986	p+m	51	17	(21d)	1	14	no effect of lactational or postweaning food intake	
Walton, 1986	p+m	129	17	(16d)	6	rc	boar exposure postweaning	effect of boar exposure postweaning;
	p+m	135	61	(16d)	26	rc	no boar exposure postweaning	no effect of boar exposure during lactation
Sterning et al., 1990	p	125	74	(10d)	24	10	no effect of body weight loss, backfat loss, litter size at three weeks, litter weight gain or season	
Tubbs et al., 1990	p+m	99	10	(8d)	4	rc	no effect of parity	
Grandhi et al., 1992	p+m	348	82	(15d)	13	15	no effect of parity, body weight loss or supplementing fat or lysine to lactational diet	

[a]Abbreviations: PAR=parity, p=primiparous, m=multiparous, N=total number of sows, NNO=number of sows not seen in oestrus before day between brackets, NSO=number of sows experiencing silent oestrus, DAY=day of checking ovarian state (postweaning), rc=repeated checking

Silent oestrus

Occurrence of ovulation without detection of oestrus may have two somewhat interrelated reasons. Signs of oestrus may be insufficient to detect oestrus, and secondly, the observation of the herdsman may be inaccurate.

Table 1 shows that large variation exists in the incidence of silent oestrus in sows after weaning. It is also clear from this table that many factors known to influence weaning-to-oestrus interval, such as breed, nutrition, parity and season, do not influence expression of oestrus at ovulation. In sows, boar presence after weaning significantly reduced incidence of silent oestrus (Walton, 1986). Willemse and Boender (1966) and Hemsworth et al. (1984, 1986b) found behavioral signs of oestrus to be more pronounced in the presence of boars, and efficacy of the back-pressure test as a means of oestrus detection was increased. Pearce and Hughes (1987) found that proceptive behaviour of oestrous sows was primarily stimulated by visual cues emitted by the boar, but also by olfactory stimuli, and to a lesser extent by auditory cues. Hemsworth and Barnett (1990) summarized evidence that space allowance affected sexual receptivity, possibly via a social stress response.

Studies with pubertal gilts, showed that stress arising from elevated temperatures (Steinbach, 1972), housing in total confinement compared with rearing outdoors (Christenson and Ford, 1979a,b) and rearing in absence of a boar (Hemsworth et al., 1982a) reduced sexual receptivity.

The suggestion of a causal relationship between stress and silent oestrus is supported by the results of Hemsworth et al. (1986a). They observed a reduced oestrus detection rate and increased plasma free-corticosteroid concentrations, when space allowance was restricted. Furthermore, Esbenshade et al. (1983) showed that in ovariectomized gilts the oestradiol benzoate-induced oestrous symptoms were suppressed by synthetic glucocorticoids, and Liptrap (1970) observed shortened duration of oestrus in sows treated with glucocorticoids at d 14 of the oestrous cycle.

In conclusion, occurrence of silent oestrus and variation in its incidence increase variation in the weaning-to-oestrus interval.

Table 2. Mean, phenotypic standard deviation and range of oestrous cycle length in gilts and sows

	PAR[a]	N[a]	NC[a]	MEAN	SD[c]	RANGE	GROUP CHARACTERISTIC
Robertson et al., 1951	g	48	48	20.5	1.5	18-25	Chester White, first cycle
	g	35	35	21.0	1.0	20-23	Poland China, first cycle
Burger, 1952	g+s	nr	295	21.7	2.3	4-31	Large Black
	g+s	nr	258	21.0	3.5	4-33	Large White
Liptrap, 1970	s	8	16	21.0	0.3	20-22	
Dyck, 1971	g+s	138	161	21.0	2.8	17-33	Yorkshire
	g+s	146	257	21.7	2.1	18-35	Lacombe
Steinbach, 1972[b]	g	147	294	20.6	2.7	13-30	
Fiedler et al., 1981	s	143	nr	23.5	2.9	18-30	
Eliasson, 1989	g	313	313	21.1	1.9	12-33	first pubertal cycle
	g	287	287	20.4	2.1	11-42	second pubertal cycle
Sterning et al., 1990	s	20	20	19.6	nr	nr	first postweaning cycle
	s	20	20	20.0	nr	nr	second postweaning cycle

[a] Abbreviations: PAR=parity; g=gilts; s=sows; N=number of gilts or sows observed; NC=number of cycles observed; nr=not reported

[b] Mean, phenotypic standard deviation and range recalculated after excluding apparently double or triple cycles (cycle length > 34 days).

[c] When phenotypic standard deviation was not given, it was recalculated from the standard error of the mean.

Oestrous cycle length

The studies summarized in Table 2 show that oestrous cycle length is on average 21 d, with a standard deviation of about two days. Although breed differences in studies of Robertson et al. (1951), Burger (1952) and Dyck (1971) are highly significant, they are very small.

Liptrap (1970) observed a prolongation of oestrous cycle length by one to three days, after treatment with glucocorticoids at d 14 of the oestrous cycle. In general, however, when cessation of cyclic activity is not considered, oestrous cycle length seems to be relatively independent of the environment.

None of the cited studies discriminated within- and between-animal variation, but Dyck (1971) reported that in 72 of the 92 sows, the difference between the lengths of two subsequent cycles was one day or less, indicating that within-animal variation is very small.

Because oestrous cycle length is only involved in the weaning-to-oestrus interval in cases of a silent oestrus, and the variation in this interval is small, we conclude that the contribution of cycle length to variation in the weaning-to-oestrus interval is not important.

Interval weaning to start of cycle

Stimuli. Several factors are known to stimulate the start of the oestrous cycle, especially at puberty, but also after weaning. Boar contact has been reported to stimulate oestrus in the weaned sow, although the success depends on the length and the frequency of exposure and the kind of contact allowed. Boar presence before weaning in itself is not able to induce oestrus during lactation, unless combined with a reduction of suckling, but it reduces the interval after weaning, at least in multiparous sows (Walton, 1986; Newton et al., 1987). In the gilt, boar contact stimulates oestrus by pheromones in urine and saliva and by tactile cues (Pearce and Paterson, 1992).

Pearce and Pearce (1992) showed that contact with oestrous females significantly decreased the weaning to mating interval. Furthermore, the onset of oestrus was significantly more synchronized in sows exposed to oestrous sows, than in control or boar-exposed sows. Marked synchronisation of oestrus is also observed in social groups in the Wild Boar (Delcroix et al., 1990).

Small environmental changes, such as relocation and incidental change of feeding level, are reported to stimulate the start of the oestrous cycle (Du Mesnil du Buisson and Signoret, 1962; Paredis, 1962; Meredith, 1979).

Stimuli may act synergistically, as is shown for the various boar components on sexual behaviour (Pearce and Hughes, 1987). Relocation, and grouping of sows with avoidance of overcrowding are reported to improve efficacy of the boar effect (Hemsworth et al., 1982b), thus intensifying the stimulus.

Stimuli which affect onset of oestrus are not always effective (Karlberg, 1980). The ability of sows to respond to stimuli may decrease under influence of poor nutrition, poor climate and housing, disease, large size of previous litter and chronic stress. These factors are outlined below in more detail.

Nutritional effects. Metabolic state is one of the most important factors influencing the animal's ability to respond to stimuli which affect onset of oestrus, and it involves both effects of feeding and condition. Sows may remain anoestrous or show a delayed return to oestrus after weaning when nutrition during lactation is inadequate (Maclean, 1968). Nutrition in previous stages of reproduction (pregnancy, previous litters, puberty) may also be of importance (Cole, 1990).

Nutritional inadequacy may arise in many ways, for there may exist deficits of energy (Reese et al., 1982a,b; King and Williams, 1984a), protein (O'Grady and Hanrahan, 1975; Brendemuhl et al., 1987, 1989) or other nutrients (Pettigrew and Tokach, 1991). During lactation, when demands exceeds supply with food intake, sows start to catabolize body tissue and thus lose body weight, in order to maintain milk production (Lodge, 1959). The composition of this weight loss depends on whether energy or protein is lacking (Brendemuhl et al., 1987; Mullan, 1991).

Many researchers believe that loss of body protein is more important than loss of body fat (King, 1987; Brendemuhl et al., 1989), especially in first-litter sows, because these animals are still actively growing at the time of their first lactation (King and Williams, 1984b). This may be one reason why the relationship between loss of body weight and delay of oestrus is equivocal: it depends on the composition of the mobilized tissue and the parity of the sow. Another phenomenon confounding the relation between mobilized tissue and body weight loss is that catabolized body fat is to some extent replaced by water (Black et al., 1986).

Since it is not weight loss in itself, which impairs reproduction, it may be the requirement to restore body reserves which affects the animal's ability to respond to stimuli which affect onset of oestrus. This requirement may be determined by critical amounts of body fat and protein (Cole, 1990).

When body reserves become depleted, pulsatile secretion of GnRH and thus of LH is decreased (Kirkwood et al., 1987; King and Martin, 1989) and follicular development is impaired, both due to the reduced gonadotropin release and direct effects of metabolic hormones. It has been suggested that high cortisol concentrations and chronically decreased plasma insulin and insulin-like growth factors are involved in decreased ovarian activity (Britt et al., 1988; King and Martin, 1989; Foxcroft, 1992).

Whether or not body reserves are depleted at weaning, depends on the condition at parturition (Mullan and Williams, 1989), the magnitude of the deficits, and the length of the lactation. Body condition at parturition can easily be manipulated by feeding during pregnancy. Deficits are determined by supply with food intake, and demands depending on number of piglets nursing, amount of milk produced per piglet, maintenance and additional growth requirements. However, it has often been observed that sows fed diets on an ad libitum basis during pregnancy, consumed less food voluntarily during lactation than their counterparts fed restricted during pregnancy (Mullan and Williams, 1989). Thus, lactational body weight loss increased, but the weaning-to-oestrus interval was unaffected. Voluntary food intake under ad libitum conditions is generally observed to be lower in first-litter sows than in older animals (King, 1987; Yang et al., 1989).

The first week of lactation is a transitional period and voluntary food intake has not yet reached its full capacity. Milk production in this period highly depends on body reserves (Mullan and Wiliams, 1989) and thus short lactations leave no opportunity for restoring body reserves.

Lactational effects. Length of the suckling period is generally considered as a factor influencing the weaning-to-oestrus interval. Aumaitre et al. (1976) reported that short lactatations (≤ 16 d) and long lactations (≥ 50 d) prolong the weaning-to-oestrus interval. However, this may be only an indirect effect, for other studies found no impairment after either short lactations (Pay, 1973; Svajgr et al., 1974; Kirkwood et al., 1984) or long lactations (Self and Grummer, 1958; Pay, 1973; Karlberg, 1980). Long lactations may be harmful, when lactational feed intake is insufficient, for body weight losses will then be closely associated with lactation length. Weaning shortly after farrowing causes considerable stress in sows (Varley and Foxcroft, 1990) and weaning immediately after birth causes the formation of cystic follicles in 30 to 50% of the sows (Britt et al., 1985). The associated stress may be the main reason for high average weaning-to-oestrus intervals after lactations of 0 to 10 d.

Direct effects of lactation length on interval to start of cycle may be restricted to sows returning to oestrus within one week after weaning. Due to the decreasing suckling frequency of piglets during lactation, LH pulsatile release and size of follicles gradually increase during lactation (Britt et al., 1985). Therefore, follicles of sows weaned after a long lactation, may need less time to reach ovulatory size than those of sows weaned after a short lactation. This is supported by results of Svajgr et al. (1974), who found a linear decrease of the weaning-to-oestrus interval with increasing lactation length. The reported average weaning-to-oestrus intervals indicate that a high percentage of sows was in oestrus within a week in all treatments.

Kunavongkrit (1984) reported that sows nursing small litters (2 to 4 piglets) tend to have higher serum LH concentrations during lactation than those nursing large litters (7 to 12 piglets). This may result in an increase in the weaning-to-oestrus interval with increasing number of piglets weaned, in sows with a weaning-to-oestrus interval of about a week. This is in agreement with the results of Yang et al. (1989), who only found a relationship between weaning-to-oestrus interval and litter size in sows of higher parities (90% in oestrus within a week) and not in first-litter sows (70% in oestrus within a week). The relationship was estimated as weaning-to-oestrus interval (in days) = 2.65 + .56 * litter size.

Seasonal effects. Although complete cessation of oestrous activity due to season, as observed in the Wild Boar (Mauget, 1982), is not common in the domestic pig, it is obvious from the survey of Claus and Weiler (1985), that seasonal variation in the weaning-to-oestrus interval, with lowered fertility in summer, exists. Seasonal infertility, however, is a complex phenomenon, involving many aspects of reproduction, such as a lowered farrowing rate, higher incidence of embryonic loss and abortions, and irregular return to oestrus after non-successful mating.

Many factors contribute to a seasonal pattern in fertility. Increasing daylength is obviously involved, for Claus et al. (1984) were able to reduce the prolonged weaning-to-oestrus interval during summer by artificially decreasing daylength. Also, Sterning et al. (1990)

observed distinct seasonal differences in numbers of sows ovulating and showing standing oestrus. They proposed that the rapid changes in daylength during spring and fall in Sweden were responsible.

In addition, high ambient temperatures, mainly during summer, may cause stress responses in sows, which reduce reproductive function (Hennessy and Williamson, 1984; Hemsworth et al., 1982b). Elevated temperatures, perhaps causing heat stress, prior to oestrus may inhibit oestrous behaviour and ovulation. Elevated temperatures during lactation reduce voluntary food intake and increases lactational weight loss (Armstrong et al., 1986; Lynch and Kerney, 1986).

It is generally observed that first-litter sows suffer more from summer infertility, than older sows (Hurtgen and Leman, 1981; Szarek et al., 1981; Britt et al., 1983). Furthermore, seasonal infertility is not common in all herds, and management factors can overcome it to a some extent, as in the experiment of Cox et al. (1983), in which supplementing 10% fat to lactational diets diminished the increase in average weaning-to-oestrus interval during summer. We propose therefore, *that increasing daylength causes a higher sensitivity of sows to environmental factors delaying onset of oestrous activity.* This is supported by the observation in the wild boar that, in addition to photoperiod, environmental factors, such as availability of food, control oestrous activity (Mauget, 1982).

Effects of stress. When animals are no longer able to adapt to environmental changes, behavioral and physiological mechanisms are activated, in order to maximize the chance of survival (Moberg, 1985).

Ryan and Raeside (1991a,b) reviewed evidence concerning effects of corticosteroids on reproductive function, and it appeared that various pathways are involved. Adrenocorticotrophic Hormone (ACTH) and/or corticosteroids are able to depress the expression of oestrous behaviour, and also block the pre-ovulatory release of LH and subsequent ovulation. Furthermore, elevated levels of corticosteroids of sufficient duration suppress the oestrogen synthesis in the ovary during follicular development. These effects lead to development of small or large multiple ovarian cysts, which are well-known to cause anoestrus or abnormal oestrous behaviour (Nalbandov, 1952; Wrathall, 1980).

There are various factors which may cause a physiological stress response in pigs, such as social stress, like mixing into new social groups, or overcrowding (Hemsworth and Barnett, 1990); aversive handling by humans (Hemsworth et al., 1991); parturition and weaning, especially when applied a short time after parturition (Varley and Foxcroft, 1990); undernutrition (Appleby and Lawrence, 1987); transportation and relocation (Dalin et al., 1988; Nyberg et al., 1988) and certain housing conditions (Barnett and Hemsworth, 1991). The magnitude of the effects of stress on reproduction is determined by the timing, duration and magnitude of these stress responses.

Diseases may also cause infertility. This may be an indirect effect, caused by stress responses, or a direct effect, when the disease affects the genital tract. Rasbech (1969) summarized infectious diseases causing reproductive failure, but reported that all of them act on aspects of reproduction other than oestrous activity, such as conception, embryonic mortality, early and late foetal death, and perinatal and postnatal death. Therefore, direct effects of infectious diseases on the onset of oestrous cycle may not be important.

In conclusion, variation in the weaning-to-oestrus interval is mainly determined by variation in 'Interval weaning to start of cycle'. Start of cycle after weaning may be delayed by severe losses of body reserves, seasonal effects and physiological stress responses.

Genetic variation in the weaning-to-oestrus interval

Variation in the weaning-to-oestrus interval appeared to be mainly determined by variation in 'Incidence of silent oestrus' and 'Interval weaning to start of cycle'. Thus, we do not expect 'Interval start of cycle to oestrus' and 'Oestrous cycle length' to contribute to genetic variation. 'Incidence of silent oestrus' may have a genetic component, but there is no direct evidence, such as breed differences, in literature to support this.

From reviewing the literature on 'Interval weaning to start of cycle', we can draw two main conclusions. First, although it seems to be a continuous trait, it has certain characteristics of a discrete variate. With adequate stimulation in the absence of severe body weight losses or stress, cyclic activity starts soon after weaning, with some small variation induced by lactation

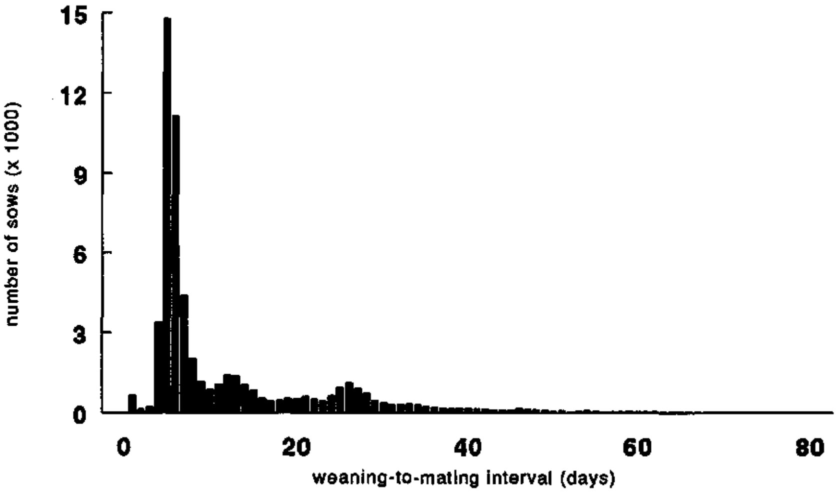

Figure 2. Distribution of weaning-to-oestrus intervals shorter than 80 days in data of 57800 first-litter sows, collected between 1984 and 1993 on Dutch commercial farms. Weaning-to-oestrus intervals ranged from 1 to 197 days.

length and litter size, because suckling, which prevents resumption of cyclic activity, disappears at weaning. In case of severe body weight losses or stress, suckling is not the only limiting factor, and onset of cyclic activity is delayed to an extent that is dependent on the severity of the problems, which means an enormous increase in variation. Therefore, we distinguish normal and prolonged intervals. This is supported by the distribution of numbers of sows with the same weaning-to-oestrus interval (Figure 2). Weaning-to-oestrus intervals of 5 and 6 days are much more frequent, than one would expect from a continuous distribution. Hence, the peak may represent normal intervals and the tail of the graph prolonged intervals. The second conclusion is that a prolonged interval may have different causes in different situations.

We suggest therefore, that the nature of the genetic variation in the 'Interval weaning to start of cycle' is the ability of sows after weaning to respond to appropriate stimuli. The question therefore is which of the factors, that suppress this ability, may be expected to show genetic variation. Two aspects of these factors are important, namely the occurrence of such a factor, and the susceptibility of a sow to that factor.

The occurrence of stressors or a certain season is environmental, but there may be some genetic variation in the responses of sows. Literature concerning the impact of genotype on susceptibility to stressors is rare. Hemsworth et al. (1990) tested gilts for fear of humans and measured five variables of behaviour. Although the data set was limited (425 sows) they estimated heritabilities and found 'time to physically interact with the human in the test', to be moderately heritable ($h^2 = .38 \pm .19$). Physiological characteristics were not measured. Hennessy et al. (1988) found large and repeatable differences in adrenal response to ACTH among individual pigs of the same age, sex, weight and genetic strain. They also found that the 15% animals with the highest adrenal responsiveness had slower growth and worse feed conversion than the 15% lowest responders (Hennessy and Jackson, 1987). Wan et al. (1994) showed that incidence of infertility was lower, and the farrowing rates higher in gilts with low adrenal response than in gilts with a high adrenal response. High responders were also more likely to suffer from seasonal infertility. These studies suggest the existence of genetic variation in physiological responsiveness to stressors, affecting metabolism and reproduction. To which extent the nature of the observed individual variation is genetic, needs further study.

Unlike season and stress, both the occurrence of a severe loss of body reserves, and the susceptibility of a sow to severe body weight loss, may have genetic components, but it is very difficult to discriminate between them. Genetic variation in voluntary feed intake, backfat depth and litter size may contribute to genetic variation in the occurrence of severe losses of body weight. Whether or not genetic variation in susceptibility exists can not be concluded from the literature, but it can not be ruled out.

If weaning-to-oestrus intervals can be distinguished in normal and prolonged intervals, then a genotype-environment interaction is involved to a very large extent. How much of the genetic variation in those underlying traits is reflected in genetic variation of the weaning-to-oestrus interval is completely dependent on the environment, determined by management, ambient temperature, feed composition, feeding level and other aspects. Both in an extremely favourable and an extremely unfavourable environment, no genetic variation will be observed, because in the one environment all animals will have a normal interval and in the other all sows will remain anoestrous. In intermediate environments, some families are more likely to have severe losses of body reserves than other families, or may be more affected by stressors than other. This can be observed as genetic variation in the 'Interval weaning to start of cycle' and thus in the weaning-to-oestrus interval.

The fact that in nucleus breeding herds, sows not in oestrus within two to four weeks after weaning are commonly culled, implies a strong genetic selection for sows which return to oestrus soon after weaning. However, a rather large genetic variation in the weaning-to-oestrus interval can still be observed (Fahmy et al., 1979; Molenaar and Van der Steen, 1983; Petrovicová et al., 1988; Ten Napel et al., 1992), compared to other fertility traits. Apparently, animals which are more likely to have a prolonged interval still contribute to the next generation.

Selecting parents for the next generation in sire lines, to achieve minimal backfat and high growth rates, is mainly based on production traits. In dam lines, reproduction traits are also involved. These selection methods may influence the ability of a sow to raise a litter, especially the first litter.

Genetic selection for minimal backfat is partially selection of animals with a low voluntary feed intake, at least during growth (Fowler et al., 1976; Vangen, 1980; Kanis, 1988). Sows from these strains may have reduced lactational feed intake capacity, which causes severe body weight losses during lactation, and subsequently a prolonged interval between weaning and oestrus. A genetically reduced appetite has also been suggested by Cole (1990) and Mullan (1991).

Furthermore, it has been suggested that primiparous sows of genetically improved strains of lean pigs have low body fat reserves at parturition and therefore reach detrimental depletion earlier than other sows (Mullan and Williams, 1989; Cole, 1990).

Thirdly, genetic selection for high growth rate at a fixed age is mainly selection of animals with a higher mature weight, as Taylor (1985) summarized. Selection against backfat at market weight may also favour late-maturing animals (Eliasson et al., 1991). These animals reach puberty at a later age (Eliasson et al., 1991; Rydhmer et al., 1992), but are generally mated at the same age as their earlier-maturing contemporaries. At the time of first lactation, the former animals need more energy and protein for growth of their own body. Consequently, they may reach harmful depletion sooner than earlier-maturing sows.

Among the reproductive traits often selected are litter size, 21-day litter weight and weaning litter weight. The latter two are involved to select for milk production ability, which is very difficult to measure in a direct way. A selection experiment based on an improved 'sow productivity index', including litter size and adjusted 21-day litter weight, showed an increased body weight loss in selection line sows, with a subsequent delay in return to oestrus after weaning (Shurson and Irvin, 1992). This suggests that genetic variation in milk production capacity is an important explanation of genetic variation in the 'Interval weaning to start of cycle'. The same may hold for genetic variation in number of suckling piglets.

Conclusion

This review indicates that genotype does not impact on the weaning-to-oestrus interval in a direct way, but that it exerts its influence in an indirect way through genetic variation in susceptibility to factors prolonging 'Interval weaning to start of cycle'. Genetic variation in the animal's susceptibility to severe depletion of body reserves, and stressors may explain the observed genetic variation in the weaning-to-oestrus interval.

The proposed model emphasizes that the weaning-to-oestrus interval should not be considered in isolation, but that it is integral to the physiological processes in the body. This consideration may help to explain apparently inconclusive results. Clearly, additional research is needed to confirm the hypotheses presented in this review.

Acknowledgement

The authors would like to thank J.H.A. te Brake, E.W. Brascamp and T. van der Lende for discussion and careful reading of the manuscript.

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Chapter 3

Genetics of interval from weaning to estrus in first-litter sows: Distribution of data, direct response of selection and heritability

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Published in Journal of Animal Science 73 (1995) 2193

Abstract

A selection experiment with a selection and a control line maintained for eight generations, was set up to study efficacy of selection for a short interval from weaning to estrus after weaning the first litter and to estimate genetic variation in the Dutch Landrace population. Intervals were recorded without truncation (i.e. intervals up to 234 d were observed). A mating scheme with 10 mating groups was used to avoid inbreeding. Distribution of intervals from weaning to estrus was described by a mixture of a normal and an exponential distribution. Between lines, both underlying distributions were similar, but the contribution to the total distribution was different. From generation 4 and onwards, intervals were significantly shorter in the selection line than in the control line. Variances within lines, generations, and mating groups varied to a large extent. Response per unit selection differential was calculated for original data and three sets of transformed data, both with and without correction for unequal subclass numbers. Standardized responses were more precise and linear, when data were log-transformed, and when corrected for unequal subclass numbers. The assumed best estimate of the realized heritability was .17. The heritability in the foundation population was estimated at .36 ± .05, using an animal model including all genetic relationships in the data. It was concluded that genetic selection decreases the average interval from weaning to estrus by reducing the number of sows with a record in the exponential part of the distribution.

Key words: Sows, Postweaning Estrus, Genetics, Reproduction, Selection

Introduction

Considerable variation among sows exists in the time between weaning and first observed estrus, and this variation is most obvious after weaning the first litter (Hurtgen and Leman, 1981; Clark et al., 1986; Maurer et al., 1985). Genotype is considered to be one of the causes of this variation. Dyck (1971), Aumaitre et al. (1976) and others observed differences between breeds or breed crosses in average interval from weaning to estrus. Heritability of interval from weaning to estrus estimated in multiparous sows is approximately .2 (Fahmy et al., 1979; Petrovicová et al., 1988). Heritability estimates of the farrowing interval, which includes the interval from weaning to estrus, are somewhat lower at approximately .1 (Johansson, 1981; Johansson and Kennedy, 1985; Vangen, 1986). Both between- and within-breed variation confirm that genotype affects resumption of cyclic activity after weaning.

The purpose of the selection experiment reported herein was to estimate genetic variation in the Dutch Landrace population and to study efficacy of selection for a short interval from weaning to estrus after weaning the first litter. Efficacy of selection was estimated by calculating direct response of selection and comparing phenotypic distributions of intervals from weaning to estrus.

Experimental procedures

General. A selection experiment was started in 1980 involving two closed lines of Dutch Landrace pigs. One line was selected for a short interval from weaning to estrus and the other was a control line in which selection was avoided, to maintain genetic variation of the foundation population and to enable correction for environmental trends. Foundation animals (n = 472) were pairs of gilts, randomly chosen from litters of 235 unrelated dams. From each pair of litter mates, one gilt was randomly chosen and assigned to the selection line and the other was assigned to the control line. Gilts were purchased in 10 groups, with all gilts in a group born in the same week. Week of birth of two successive groups differed by 5 wk. All gilts in a group were purchased at the same time, but age at purchase varied from 5 to 7 mo across groups.

A mating scheme, consisting of 10 mating groups, was set up to avoid inbreeding as much as possible (Table 1). Several AI boars were used across each line to inseminate foundation animals and gilts of the first generation of the first five mating groups. Afterward, lines were kept closed. Sows were selected within their mating group, and gilts and boars were randomly chosen from their litters. Gilts and boars were identified by the mating group of their dams, but boars were always used as breeders in a different mating group, either from the same generation if the boar came from mating group 0 to 4, or from the next generation if the boar

Table 1. Descent of animals per generation and mating group (generation-mating group dam x generation-mating group sire), with AI referring to artificial insemination

	Mating Group									
Generation Progeny	0	1	2	3	4	5	6	7	8	9
1	00 x AI	01 x AI	02 x AI	03 x AI	04 x AI	05 x AI	06 x AI	07 x AI	08 x AI	09 x AI
2	10 x AI	11 x AI	12 x AI	13 x AI	14 x AI	15 x 11	16 x 12	17 x 13	18 x 14	19 x 10
3	20 x 19	21 x 15	22 x 16	23 x 17	24 x 18	25 x 20	26 x 21	27 x 22	28 x 23	29 x 24
4	30 x 25	31 x 26	32 x 27	33 x 28	34 x 29	35 x 32	36 x 33	37 x 34	38 x 30	39 x 31
5	40 x 38	41 x 39	42 x 35	43 x 36	44 x 37	45 x 43	46 x 44	47 x 40	48 x 41	49 x 42
6	50 x 46	51 x 47	52 x 48	53 x 49	54 x 45	55 x 50	56 x 51	57 x 52	58 x 53	59 x 54
7	60 x 55	61 x 56	62 x 57	63 x 58	64 x 59	65 x 62	66 x 63	67 x 64	68 x 60	69 x 61
8	-	-	72 x 69	-	74 x 66	-	76 x 70	-	78 x 72	-

came from mating group 5 to 9. Also within mating groups, matings between related individuals were avoided as much as possible.

In each generation, gilts of a particular mating group were inseminated in the same 4-wk period of the year. The experiment consisted of the foundation population of purchased gilts, seven generations of selection, and in addition, one generation with only four mating groups with relaxed selection.

Managing Procedures. Gilts were moved to the mating unit at 31 to 36 wk of age and housed in pens of four contemporary gilts opposite boar pens. They were checked for estrus twice daily. Those that were not seen in estrus within 3 wk were treated with 400 IU of PMSG + 200 IU of HCG intramuscularly (PG600®; Intervet Nederland bv, Boxmeer, The Netherlands) and those not served within 4 wk after entering the mating unit were excluded from the experiment. Mated gilts were girth tethered in a gestation barn, between 1 and 2 wk after the end of the mating period. Pregnancy was checked ultrasonically at 28 and 35 d after mating. Non-pregnant gilts were excluded from the experiment.

Table 2. Number of sows with an observed interval from weaning to estrus, within lines and generations, both absolute (n), and as a fraction of total number of replacement gilts at moving to the rearing pen

	Selection line		Control line	
Generation	n	% total	n	% total
0	125	53^a	118	50^a
1	86	40^a	86	39^a
2	113	55^a	116	53^a
3	119	55^a	106	49^a
4	156	63^a	118	48^b
5	161	61^a	144	51^b
6	150	60^a	136	48^b
7	142	53^a	146	55^a
8	63	56^a	48	46^a
total	1115	55^a	1018	49^a

^{a,b} Numbers of sows within a row lacking a common superscript letter differ ($P<.05$).

Sows were moved to farrowing crates about 1 wk before the expected farrowing date. Litter size was standardized at parturition within mating group and line at an average of eight pigs, whenever possible. Pigs were weaned between 32 and 38 d of lactation and sows were moved to the mating unit and housed individually. Sows in the mating unit were removed from the experiment on Thursdays after showing estrus, because interval from weaning to estrus had been established. All sows not yet seen in estrus were moved to a new pen every week. Sows remained in the mating unit until they showed estrus spontaneously. In every 10th pen, a boar was housed to stimulate onset of estrus. Treatment with hormones to induce estrus was not practiced. Checks for estrus were made twice a day, but a teaser boar was used only in the morning.

Most of the gilts and sows removed from the experiment were slaughtered and their reproductive tracts were examined. If a sow was slaughtered between 3 and 17 d after showing estrus, and corpora albicantia were observed on the ovaries, it was assumed that the sow experienced a silent estrus, before the observed estrus.

Table 3. Number of sows per reason for not having an observed interval from weaning to estrus as a fraction of total number of sows without an interval from weaning to estrus

Category	Selection line	Control line
Death, disease	19.7	22.5
Stress	2.1	1.3
Leg problems, poor legs	10.9	13.3
Not in estrus in mating period	16.0	13.8
First mating not successful, or sow aborted	35.0	32.6
Other[a]	16.3	16.5

[a] Includes surplus at moving to mating pen as a gilt, entire litter dead at birth, entire litter dead before weaning, entire litter crossfostered, and reason not recorded.

After weaning, pigs were housed on flatdecks, until they weighed 25 kg on average. They had free access to food (12.8 MJ of ME/kg, 17.8% CP, 10.54 g/kg digestible lysine). Afterward, gilts were housed in pens of four of the same line and mating group. They were allowed to consume food ad libitum (12.0 MJ of ME/kg, 14.5% CP, 6.80 g/kg digestible lysine), until they weighed 90 kg on average. Afterward, they were fed 2.25 kg daily of the same diet. During the mating period, both gilts and sows were fed 2.5 kg per day (11.7 MJ of ME/kg, 13.5% CP, 5.95 g/kg digestible lysine). This regimen was continued during gestation, except for the last month, in which the daily ration was gradually increased to about 3 kg. Technicians were allowed to make minor adjustments in these rations by evaluating the body condition of the gilt. Sows received 1.5 kg food on the day before parturition, no food on the day of parturition and 1 kg on the 1st d of lactation. During the following 10 d feeding levels were increased and subsequently sows were allowed to consume food ad libitum, with a maximum of 6 kg daily. From generation 5 and onwards, a different lactational diet was fed (12.6 MJ of ME/kg, 16.8% CP, 7.24 g/kg digestible lysine). All animals had free access to water.

Selection Procedures. A short interval from weaning to estrus was the only criterion of selection in the selection line. In each mating group, 22 to 26 gilts per generation were randomly chosen from litters of the six to eight selected sows with the shortest intervals from weaning to estrus. From litters of the three best selected sows, eight boars were chosen. Sows in the selection line, which had been treated with hormones before puberty, were not selected.

To avoid selection in the control line, at least one gilt from each litter was reared and some additional gilts were chosen to complete the mating group in that generation, such that the number of chosen animals per sire was as equal as possible and the average interval from weaning to estrus of the dams reflected the mean of the mating group in that generation as much as possible. The latter two criteria were also used for choosing eight boars to be reared.

In both lines, gilts with leg problems after the rearing period were not mated. From the eight boars reared in each line, three were selected as mating boars, and one as a reserve, based on leg soundness and libido.

Number of sows with an observed interval from weaning to estrus per mating group in a generation varied from 4 to 24 in the selection line and from 2 to 21 in the control line. The average number of observations was 13.4 and 12.1, respectively. Numbers of observed intervals per line and generation are shown in Table 2. Numbers of sows per reason for not having an observed interval from weaning to estrus in each line are given in Table 3. Because in some generations the number of observed intervals in a mating group was too small to select sufficient dams, there was a total of 15 selection-line and 38 control-line sows selected as a dam, although interval from weaning to estrus was not observed due to crossfostering the entire litter, disease, leg, or other problems.

Statistical Methods. Agha and Ibrahim (1984) described a maximum-likelihood algorithm for estimation of parameters of a mixture of distributions, with all underlying distributions of the same type. We extended this algorithm to a mixture of distributions of different types, by using the entire density functions of the underlying distributions. This algorithm was used to estimate parameters of a mixture of a normal and an exponential distribution in the within-line distributions of interval from weaning to estrus. A grid search with steps of 1 d was performed to estimate the optimal starting position of the exponential distribution. Maximized log likelihood was used to compare different starting points. Goodness of fit was checked by performing a linear regression of observed incidence on incidence predicted with the estimated composite density function.

Within-generation differences between observations in the selection and control lines were tested with the Wilcoxon rank sum test, approximated with a normal distribution (SPSS, 1983). The hypothesis tested was that, within generations, the chance of a selection-line observation being shorter than a control-line observation, was greater than .5.

Responses, standardized for selection differentials, were calculated using means (μ), estimated within line, generation, and mating group. Boars were chosen as sires, because of the performance of their dams, and sows were selected as dams on their own performance. Thus, when dams come from mating group *b* and sires from mating group *a*, the selection differential (D) in generation *t* was calculated within lines (*l*) as follows:

$$D_{[l,t,b]} = \tfrac{1}{2} * (\mu_{[l,t-1,b];\text{dams for females}} - \mu_{[l,t-1,b];\text{females}}) + \tfrac{1}{4} * (\mu_{[l,t-2,a];\text{dams for sires}} - \mu_{[l,t-2,a];\text{dams for females}});$$

and the corresponding response (R) was as follows:

$$R_{[l,t,b]} = \tfrac{1}{2} * (\mu_{[l,t,b];\text{females}} - \mu_{[l,t-1,b];\text{females}}) + \tfrac{1}{2} * (\mu_{[l,t,b];\text{females}} - \mu_{[l,t-1,a];\text{females}}).$$

See Appendix for derivation of $D_{[t,b]}$ and $R_{[t,b]}$. In mating groups 0 to 4, sows were mated with boars of the previous generation (Table 1), so [l,t-2,a] and [l,t-1,a] in the formula for D and R, respectively, should be replaced by [l,t-3,a] and [l,t-2,a] in these cases. We took for $\mu_{[l,t-2,a];\text{dams for sires}}$, $\mu_{[l,t-2,a];\text{dams for females}}$ and $\mu_{[l,t-1,a];\text{females}}$ the average interval from weaning to estrus of all animals in the foundation population over lines, when sires were AI boars. If a dam or a sire's dam did not have a recorded interval from weaning to estrus, a record equal to the mean of the sow's mating group was assigned to that animal.

The cumulated corrected selection differential (corrected for unintentional selection in the control line) in generation *t* was calculated as follows:

$$CD_t = \sum_{i=1}^{t}\left(\frac{1}{10}\sum_{b=0}^{9} D_{[S,i,b]} - \frac{1}{10}\sum_{b=0}^{9} D_{[C,i,b]}\right)$$

and the cumulated corrected selection response in generation *t* (CR_t) was calculated as follows:

$$CR_t = \sum_{i=1}^{t}\left(\frac{1}{10}\sum_{b=0}^{9} R_{[S,i,b]} - \frac{1}{10}\sum_{b=0}^{9} R_{[C,i,b]}\right)$$

Response per unit selection differential was estimated as the coefficient of regression of CR_t on CD_t.

Cumulated corrected selection differentials and responses were also calculated after correction for unequal subclass numbers as follows:

$$CD_t = \sum_{i=1}^{t} \left(\frac{1}{10} \sum_{b=0}^{9} \frac{N_{[S,i,b]}}{13} * D_{[S,i,b]} - \frac{1}{10} \sum_{b=0}^{9} \frac{N_{[C,i,b]}}{13} * D_{[C,i,b]} \right)$$

$$CR_t = \sum_{i=1}^{t} \left(\frac{1}{10} \sum_{b=0}^{9} \frac{N_{[S,i,b]}}{13} * R_{[S,i,b]} - \frac{1}{10} \sum_{b=0}^{9} \frac{N_{[C,i,b]}}{13} * R_{[C,i,b]} \right)$$

where $N_{[S,i,b]}$ was the number of observations in generation *i* of mating group *b* in the selection line, and 13 was the average number of observations per generation in a mating group within a line.

In addition to the original data, three data sets were created using transformations. Reasons for transforming the data are explained in the discussion section. In the first set, original data were standardized within line, generation, and mating group, using the following:

$$z_{[l,t,b,i]} = \frac{(y_{[l,t,b,i]} - \mu)}{\sqrt{\sigma^2_{[l,t,b]}}}$$

where $z_{[l,t,b,i]}$ and $y_{[l,t,b,i]}$ are the transformed and the original record of animal *i* in mating group *b*, generation *t* and line *l*, respectively, μ is the overall mean, and $\sigma_{l,t,b]}$ is the variance among records of animals in line *l*, generation *t*, and mating group *b*.

In the second set, original data were transformed using a natural log transformation:

$$z_{[l,t,b,i]} = \ln(y_{[l,t,b,i]})$$

An alternative natural log transformation was applied in the third set created, which makes $z_{[l,t,b,i]}$ equal to $y_{[l,t,b,i]}$, if y is lower than 5 d, and if y is greater than or equal to 5 d, then

$$z_{[l,t,b,i]} = \frac{\ln(y_{[l,t,b,i]})}{\ln(6)-\ln(5)} - \left(\frac{\ln(6)}{\ln(6)-\ln(5)} - 6\right)$$

Both the unweighted and weighted analyses were performed on each of the four data sets.

Response per unit selection differential was also estimated within mating groups, and the standard deviation of the 10 estimates in each of the eight types of analysis, divided by the standard deviation of the estimates from the original set of data without correction for unequal subclass numbers, was used as a relative measure of precision. Absolute values of standard deviations are not informative, because the 10 mating groups are not independent. Relative values are informative, because all data sets have the same degree of dependence, and differences are only caused by the type of analysis and transformation.

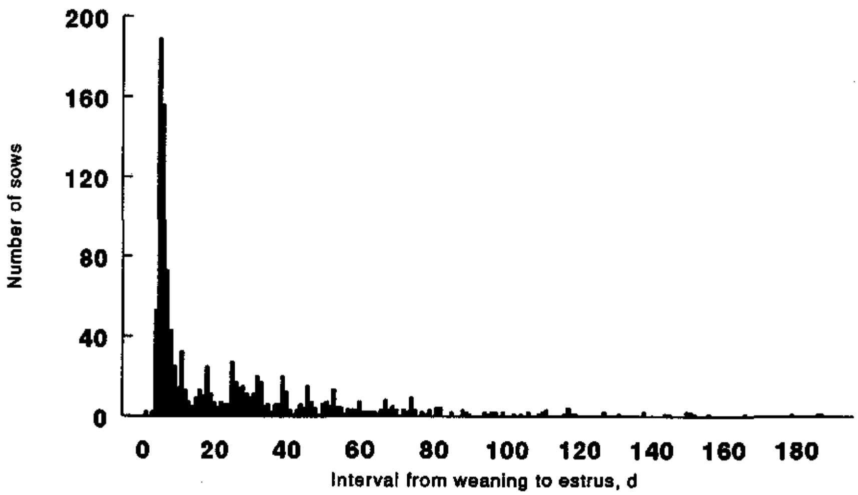
Components of variance were estimated both across and within lines, using a derivative-free restricted maximum-likelihood algorithm (Graser et al., 1987), as applied in DFREML (Meyer, 1991). The model included effects of generation and mating group combined as fixed, and animal effects as random effects. All genetic relationships between animals were taken into account. Parents of foundation animals were assumed to be unrelated.

Differences in average predicted breeding values (u) between the selection and control line were tested within generations, using a t-test. Variance of difference in generation *i* was calculated as follows:

$$V(u_{i,S} - u_{i,C}) = V(\mathbf{k}_i'\mathbf{u}) = \mathbf{k}'\mathbf{A}\mathbf{k}_i * V(\mathbf{u}) - \mathbf{k}'\mathbf{C}_{22}\mathbf{k}_i * V(\mathbf{e})$$

(Sorensen and Kennedy, 1986), where **u** is the vector of predicted breeding values, **k** is a vector of coefficients, **A** is the additive-genetic relationship matrix, $\mathbf{C}_{22}$ is the random part of the inverse coefficient matrix, and V(**u**) and V(**e**) are the genetic and residual variances, respectively, estimated across lines.

A. Selection line



B. Control line

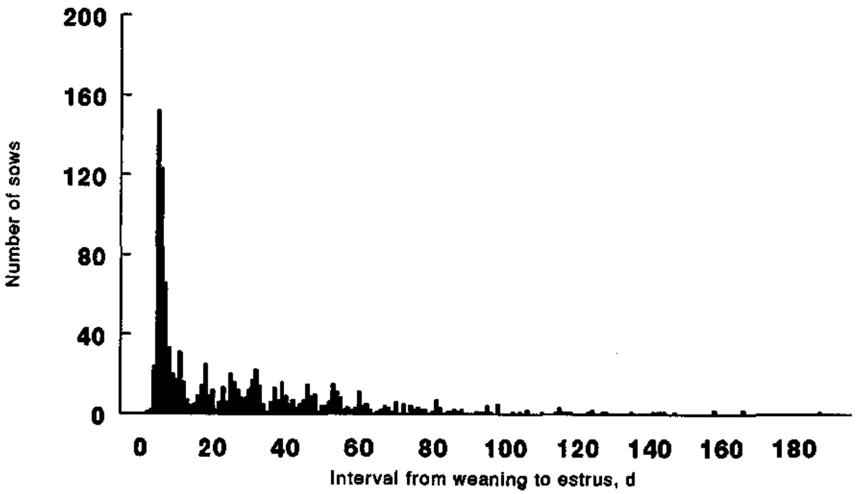


Figure 1. Distributions of intervals from weaning to estrus in the selection line (A) and the control line (B).

Results

Effects of selection on the distribution of interval from weaning to estrus were studied by comparing the within-line distributions (Figure 1). Data of all generations were combined in

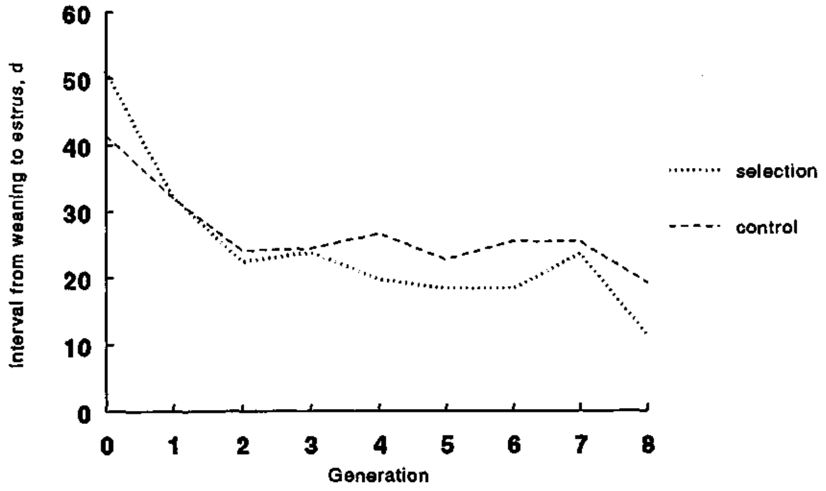


Figure 2. Average interval from weaning to estrus per generation in selection-line and control-line sows.

these distributions. Shape and mode of the distribution were not affected by selection, but the frequency at the mode of the distribution was higher in the selection line. Besides the mode, small peaks are visible every 7 d from d 11 through d 74, almost certainly caused by the managing procedure of moving anestrous sows weekly to a new pen.

Because the distribution of intervals from weaning to estrus is markedly different from known distributions of other traits, and because effects of selection on the distribution are also different, we tried to estimate a density function of interval from weaning to estrus. After comparing several types of distributions, it seemed that a mixture of a normal and an exponential distribution fitted best in both lines. It was clear from the grid search that d 5 was the optimal starting position of the exponential distribution in both lines. Estimates of parameters were almost identical over lines, except for the relative contribution of the underlying distributions to the total distribution (Table 4).

The within-generation mean in the selection line decreased markedly during the experiment, as shown in Figure 2. In the control line, the average interval from weaning to estrus decreased as well, but to a smaller extent. Although selection-line intervals were shorter than control-line intervals in generation 4 ($P < .05$), 5 ($P < .05$), 6 ($P < .01$), 7 ($P = .06$), and 8 ($P < .05$), considerable variation existed in means of mating groups within a generation. Even in the last generations some mating groups in the control line had a lower average interval from weaning to estrus than the contemporary mating group of the selection line. Variances within line, generation, and mating group, varied to a large extent, and ranged from 2 to 3,811 d^2 in the selection line, with 90% lying between 93 and 1,604 d^2, and from 1 to 3,896 d^2 in the control line, with 90% between 149 and 1,874 d^2.

In both unweighted and weighted analyses, the original data and the sets of log-transformed data gave comparable estimates (Table 5), but estimates from the set of standardized data were higher. Amount of variation in cumulated corrected response explained by linear regression on cumulated selection differentials was increased by transforming the data and by correcting for unequal subclass numbers, and was highest after applying the alternative log-transformation. The standard deviations among regression coefficients estimated within mating groups were lowest in the sets of log-transformed data.

The heritability in the foundation population, estimated with data of all subsequent generations, using an animal model, was lower when estimated across lines, than in the selection and control line separately (Table 6). Within-generation average breeding values of the selection and control lines are shown in Figure 3. Average breeding values were not different between lines in any generation.

Discussion

Distributions of interval from weaning to estrus in the selection line and in the control line could be described by the same set of functions, with only relative contributions being different. Genetic selection apparently causes a shift from the exponential part to the normal part of the distribution. Furthermore, we consider the similarity of lines, being described by a normal and an exponential part, as strong evidence for the concept of normal versus prolonged intervals (Ten Napel et al., 1995).

Table 4. Maximum-likelihood estimates of parameters of a mixture of a normal and an exponential distribution, fitted on data of interval from weaning to estrus

Item	Selection line	Control line
Normal distribution		
Fraction	.393	.314
Mean	5.569	5.627
Standard deviation	1.075	.971
Exponential distribution		
Fraction	.607	.686
Mean (=variance)	36.81	36.87
Starting position	5	5
Variation explained, %	94.9	92.9

By examining reproductive tracts after slaughter, it was established that 11.0% of selection-line sows and 9.2% of control-line sows experienced a silent estrus before the first observed estrus after weaning. Apparently, incidence of a silent estrus was not reduced by selection for a short interval from weaning to estrus. It was not possible to fit silent estrus into the density function, because the contribution of the distribution representing observations with a silent estrus consistently decreased to zero. Examination of the distribution of sows with a silent estrus showed that it was different from the overall distribution, because the normal part of the distribution is missing. It seems that in this experiment, sows with a prolonged interval were more prone to silent estrus, than sows with a normal interval. However, this may be an artifact, caused by the procedure of weekly moving sows to a new pen. If that occurred before estrus, but after the start of cyclic activity, concurrent stress reactions may have inhibited expression of estrus. Sows were moved on d 7, 14, 21, and so on. Numbers of sows in estrus are lowest on these days in both lines (Figure 1). These concurrent stress responses, however, may have stimulated onset of estrus before start of cyclic activity, because numbers of sows in estrus are highest at d 4 after relocating sows (d 11, 18, 25, and so on, after weaning). Examination of the reproductive tracts also showed that

Table 5. Response per unit selection differential (b) estimated over mating groups, relative precision (a, in %), and percentage of variation in cumulated corrected response explained by linear regression on cumulated corrected selection differentials (R^2), both for unweighted selection differentials and responses, and after weighting with corresponding subclass numbers

	Unweighted			Weighted		
Item	b	a(%)^x	R^2	b	a(%)^x	R^2
Original data	.115	100	20.2	.099	92	39.9
Standardized data	.245	158	23.2	.339	175	48.1
Log transformed data	.140	61	37.1	.163	70	62.1
Log transformed data (alternative)	.145	59	44.2	.171	70	68.1

^{x} Standard deviation of 10 estimates of the response per unit selection differential, estimated within mating groups, expressed relative to the standard deviation in original data using original differentials and responses.

lactational estrus was very rare: only two sows in the selection line, and one sow in the control line were found to have ovulated during lactation.

A high number of sows was removed from the experiment due to the experimental design, which did not allow matings after the mating period (Table 2 and Table 3). This reduced the selection intensity in the selection line, but probably not the selection differential in this particular case. Almost all selected dams had an interval from weaning to estrus of 4 to 6 d. It is clear from Figure 1, that an increase in number of observations will have only a small effect on the mean of the selected animals. Unless the culled animals would have had intervals from weaning to estrus, which are different from those observed, thus causing a change of the group mean, the selection differential would not have been very different, if no animals were removed from the experiment due to the experimental design.

In generation 4, 5, and 6, and also across generations, more sows from the control line were removed before observing the interval from weaning to estrus, than from the selection line. Distribution of animals over categories of culling was not different between lines, but differed between generations ($P<.05$). Of all the animals removed from the experiment before an interval from weaning to estrus was observed, 12% were removed before entering the mating pen, 74% were removed between entering the mating pen and farrowing, and 14% after farrowing. The distribution over these groups was not different between lines.

Table 6. Structure of data set used, animal-model estimates of variance components, and heritability in the selection and control line combined and separately

Item	Combined	Selection line	Control Line
Animals in pedigree	2,750	1,385	1,332
Sows with data	2,133	1,115	1,018
Inbred animals	876	461	415
Average coefficient of inbreeding, %	.288	.328	.216
Additive genetic variance, d^2	271	310	352
Residual variance, d^2	480	403	469
Heritability	.361	.435	.429
Standard error heritability	.052	.085	.076

The observation of an exponential distribution contributing to the total distribution implies that small samples show large variation in sample mean and variance, due to the fact that extreme values have large impact. Drawing 100 samples of size 13 from the estimated mixed distribution of the selection line yielded sample variances ranging from 58 to 7,528; 90% of the sample variances were between 217 and 1,564. Variances within line generation, and mating group, observed in the experiment, were somewhat smaller, but the range was comparable. We therefore assumed that heterogeneity of variances was due to the small size of mating groups within generations.

The relative contribution of the normal distribution (Table 4) is an average value over generations. This parameter, however, is likely to increase gradually during the experiment, due to selection. Because variance is dependent on the fraction of the normal distribution, it will decrease when the amount of the normal distribution increases, thus causing heterogeneous variances. Calculating variances with the moment-generating function of the composite density function yields a decrease in variance of 26% when the amount of the normal distribution increases from 20 to 50%. Such a decrease is negligible to the observed

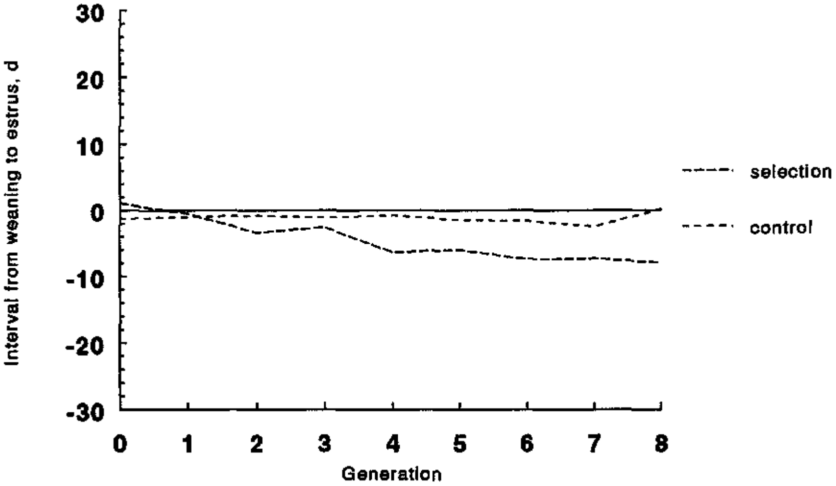


Figure 3. Average breeding values for interval from weaning to estrus per generation in selection-line and control-line sows with a interval from weaning to estrus observed.

variation in within-generation variances. In the animal-model analysis, additive-genetic and residual components of variance were indeed estimated to be somewhat lower in the selection line than in the control (Table 6).

Given the exponential characteristics of the distribution, testing significance of differences in observations between lines using the Wilcoxon Rank Sum Test is more advantageous than comparing means, because the impact of extremes is reduced by taking into account only the rank and not the magnitude. This test accounts for non-normality, but ignores variation due to genetic drift. The alternative test of between-line differences in average predicted breeding values accounts for variation due to genetic drift, but it is implicitly assumed that differences are normally distributed. Predicted breeding values, however, should be interpreted with caution, because they are a function of estimates of the components of variance and depend on whether the model is correct.

Heritabilities calculated from REML estimates of variance components are somewhat higher than those reported in literature (Fahmy et al., 1979; Petrovicová et al., 1988), and confirm that there is a substantial amount of additive genetic variation in interval from weaning to estrus, which is in contrast to other fertility traits, such as litter size (Johansson and

Kennedy, 1985; Bichard and David, 1985). The difference between the estimate over lines and estimates within lines is that the latter two are based on parent-offspring and fullsib/halfsib information only, whilst the former includes also information from the changing contrast between lines, due to selection. Fitting a line-generation-mating group interaction when analyzing the entire data set yielded similar estimates as the within-line analyses.

The responses per unit selection differential were calculated using means, as described. The precision when applied to original data, therefore, may be lowered in the case of an exponentially distributed trait, because of the large variation in sample means and variances. The first transformation was applied to correct for heterogeneity of variances. The second was used to correct for the exponential characteristics of the data. The third transformation was used, to take into account that data originated from a mixture of distributions, and in fact reduces the value of a difference of one day, when it is further away from a normal interval. The transforming function f is chosen such that $f(5) = 5$ and $f(6) = 6$, which means that normal intervals are not transformed, in fact.

Standardizing the original data appeared to be not a good method to increase the precision of the standardized response, for the variation in within-mating-group estimates was even increased relative to the variation in estimates from original data. The relative precision was highest in the third set of transformed data, and percentage of variation in the cumulated corrected response explained by linear regression on cumulated corrected selection differentials was highest, so we assume the alternative log-transformation in combination with the correction for unequal subclass numbers to be the best estimate.

The response per unit selection differential can be considered as an estimator of the realized heritability, although the selection procedure applied is slightly different from individual selection. It is, however, strictly not unbiased, because parents were unrelated only in the first generation (Falconer, 1989). The realized heritability of .17 is lower than the heritability of .36 in the base population. A commonly used explanation for such a difference is that the latter is overestimated because of common environmental covariances between relatives. This is unlikely in this experiment, because litter mates were generally reared in different pens. A more likely explanation is that the environment of selection was not constant throughout the experiment. Management procedures after weaning were applied very strictly, but procedures during rearing, gestation and lactation have been changed during the experiment, which may have interfered with selection.

Use of an algorithm as applied in the DFREML-programs implies the assumption of data having a multivariate normal distribution, which is not correct for interval from weaning to estrus. To study effects of this invalid assumption, we simulated 200 data sets with 50 sires, 5 dams per sire and 4 offspring per dam. In the first 100 sets, breeding values for sires and dams were drawn from an exponential distribution with σ as variance, and residuals from an exponential distribution with σ as variance. In the next 100 data sets breeding values were drawn from normal distributions, with σ and σ as variances. Data of progeny were simulated as follows:

$$\text{Phenotype} = .5 * BV_{sire} + .5 * BV_{dam} + \text{residual}$$

The heritability calculated with σ and σ was .25. Heritabilities calculated with simulated breeding values were .251 ± .040 and .246 ± .020 in the exponential and normal distributed data. Estimated heritabilities were .266 ± .090 and .240 ± .061, respectively. Standard errors of means were calculated with variances between replicates. We concluded that with exponentially distributed data, estimates are not biased ($P < .05$), but standard errors are larger ($P < .05$) than those from normally distributed data.

Implications

The results of this experiment indicate that genetic selection reduces average interval from weaning to estrus by decreasing the number of sows with a prolonged interval, without affecting incidence of silent estrus. Genetic selection as applied in this experiment may be a useful tool for decreasing incidence of prolonged intervals, but it may not be very efficient.

Acknowledgement

The authors would like to thank J.H.A. te Brake, B. Kemp, T.H.E. Meuwissen, and R. K. Johnson for discussion and careful reading of the manuscript.

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Appendix

Selection differential and response will be derived from the expected average performance of progeny after selecting their parents. If both females and males can be measured, the expected average performance (μ) of progeny in generation *t* is as follows

$$E(\mu_{[t]}) = \mu_{[t-1]} + \tfrac{1}{2} * h^2 * D_{[t-1];\mathrm{sires}} + \tfrac{1}{2} * h^2 * D_{[t-1];\mathrm{dams}},$$

where D is the superiority of the selected sires or dams, as a deviation from $\mu_{[t-1]}$, and h^2 is the heritability.

When expression of the trait is restricted to females, D_{sires} can not be determined directly, and $\mu_{[t-1]}$ will be based only on the performance of females. Assuming $\mu_{[t-1];\mathrm{females}}$ to be an unbiased estimator of $\mu_{[t-1]}$, an alternative estimator of D_{sires} is the difference between the expected mean of the sires and the mean of the females from which the dams were selected, the former representing the mean of the sires and the latter the population mean. In the experiment reported herein, sires were assigned to the mating group of their dam, but they always mated gilts of a different mating group. Consider line *l* and let *a* be the mating group of the sires, *b* the mating group of the dams, mated by sires from mating group *a* in generation *t-1*, and *c* the mating group of the sires in generation *t-2* of the sires in mating group *a*. Thus, the expected average performance of the progeny in generation *t* is as follows:

$$E(\mu_{[l,t,b];\mathrm{females}}) = \mu_{[l,t-1,b];\mathrm{females}} + \tfrac{1}{2} * h^2 * D_{[l,t-1,a];\mathrm{sires\ for\ females}} + \tfrac{1}{2} * h^2 * D_{[l,t-1,b];\mathrm{dams\ for\ females}}.$$

The expected mean of the sires is then

$$E(\mu_{[l,t-1,a];\mathrm{sires}}) = \mu_{[l,t-2,a];\mathrm{females}} + \tfrac{1}{2} * h^2 * D_{[l,t-2,a];\mathrm{dams\ for\ sires}} + \tfrac{1}{2} * h^2 * D_{[l,t-2,c];\mathrm{sires\ for\ sires}}.$$

Again, $D_{[l,t-2,c];\mathrm{sires\ for\ sires}}$ can not be determined directly, but selection of sires for sires is equivalent to selection of sires for females, so

$$D_{[l,t-2,c];\mathrm{sires\ for\ sires}} = D_{[l,t-2,c];\mathrm{sires\ for\ females}}.$$

A statistic exists, which includes the latter term, namely $\mu_{[l,t-1,a];\text{females}}$, because

$$E(\mu_{[l,t-1,a];\text{females}}) = \mu_{[l,t-2,a];\text{females}} + ½ * h^2 * D_{[l,t-2,a];\text{dams for females}} + ½ * h^2 * D_{[l,t-2,c];\text{sires for females}}.$$

Therefore, an estimator of the expected mean of the sires is as follows:

$$\hat{E}(\mu_{[l,t-1,a];\text{sires}}) =_{[l,t-1,a];\text{females}} - ½ * h^2 * \hat{D}_{[l,t-2,a];\text{dams for females}} + ½ * h^2 * \hat{D}_{[l,t-2,a];\text{dams for sires}},$$

and an estimator of $D_{[l,t-1,a];\text{sires}}$ is as follows:

$$\hat{D}_{[l,t-1,a];\text{sires}} = \hat{E}(\mu_{[l,t-1,a];\text{sires}}) - \hat{\mu}_{[l,t-1,b];\text{females}}.$$

Substituting the expectation of these terms for $D_{[l,t-1,a];\text{sires}}$ in the expectation of the progeny mean yields

$$\begin{aligned} E(\mu_{[l,t,b];\text{females}}) = {} & ½ * \mu_{[l,t-1,b];\text{females}} + ½ * \mu_{[l,t-1,a];\text{females}} \\ & - ¼ * h^2 * D_{[l,t-2,a];\text{dams for females}} + ¼ * h^2 * D_{[l,t-2,a];\text{dams for sires}} \\ & + ½ * h^2 * D_{[l,t-1,b];\text{dams for females}}. \end{aligned}$$

Selection differential and response, as defined in the paper, can easily be derived from this equation.

Chapter 4

Genetic relationships among production traits and rebreeding performance

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Accepted for publication in Journal of Animal Science (in press)

Abstract

We studied effects of selection for increased daily gain, reduced backfat, increased number of piglets born alive, and increased 21 d litter weight on interval from weaning to farrowing (IWF) of two commercial populations of purebred Large White (LW) and Landrace (LR) lines with each represented in two farms. The analysis took into account that normal and prolonged intervals could be distinguished. Distributions of IWF could be described by a mixture of a normal and an exponential distribution. Observed intervals were transformed to the probability of being a prolonged interval, using the mixed density function. Incidence of normal intervals was less in LR than in LW sows, and was least in first-litter sows. Heritability estimates of IWF ranged from zero to .24 across parities and farms. Genetic trend within breed and farm was different from zero ($P < .05$) for each trait under selection, except backfat on Farm 2. Genetic correlations between the traits under selection and IWF were inconsistent across farms. Differences in estimated breeding value for the traits under selection between sows with a normal and a prolonged interval were only significant on Farm 1 in the Large White breed, when only observed intervals were analyzed. Including culled sows in the analysis as sows with a prolonged interval yielded consistent differences for average daily gain and backfat, such that genetic selection for improved production would increase the liability for a prolonged interval. Culling sows for delayed estrus apparently overcame this problem on Farm 2, but not on Farm 1, on which a trend of increasing incidence of prolonged intervals was observed.

Key Words: Selection, Growth, Reproduction, Pigs

Introduction

Genetic selection for increased average daily gain and decreased backfat thickness, has proven to be a successful method, in both selection experiments and breeding programs

(Leymaster et al., 1979; Cameron, 1994; Kuhlers and Jungst, 1993). Decreased reproductive performance as a correlated response has been studied (Morris, 1975; Vangen, 1980; Kerr and Cameron, 1995), with most attention given to litter traits, rather than to rebreeding performance. Estimated genetic correlations among reproduction and production traits have generally been reported low (Johansson and Kennedy, 1983; Kersey DeNise et al., 1983; Rydhmer et al., 1995).

It is more likely that genetic selection for production impairs rebreeding performance than litter size and weight. Pathways by which this association may occur are discussed by Ten Napel et al. (1995a). Although the interval from weaning to estrus is a continuous trait, normal and prolonged intervals can be distinguished (Ten Napel et al., 1995a,b). This may also be possible for the interval from weaning to mating or farrowing.

In this paper we study the genetic relationships among traits under selection and rebreeding performance. We aimed to take into account that normal and prolonged intervals can be distinguished, and we therefore present a method to transform the interval from weaning to farrowing to a normal or a prolonged interval. The transformed trait, occurrence of a prolonged interval, has characteristics of a binary trait. Since it is extremely difficult to estimate a genetic correlation between a continuous and a binary trait, we study genetic relationships with the occurrence of a prolonged interval by estimating the contrast in average estimated breeding value between sows with a normal and a prolonged interval from weaning to farrowing. The estimated genetic relationships are compared with estimates of genetic correlations among the test traits and the untransformed interval from weaning to farrowing, ignoring the distinction between normal and prolonged intervals.

Materials and methods

Description of populations and management. Data on purebred Large White and Landrace pigs from two closed commercial breeding herds in Nebraska were used to evaluate the effects of genetic selection for improved production and reproduction on rebreeding performance of first-, second-, and third-litter sows. Pigs included in the data were born between December 1988 and March 1994 on Farm 1 and between June 1989 and March 1994 on Farm 2.

Purebred populations within farms were selected for increased daily gain, and decreased backfat depth using estimated breeding values calculated from the performance of an animal and its full and half sibs. In addition, each population was selected for number of piglets born alive, and 21-d litter weight, using estimated breeding values calculated from the dam's performance only, after including data from all available parities. During the period of this study all replacement animals for each farm were selected from pigs born and tested on that farm.

Animals were tested for average daily gain and backfat in contemporary groups, with pigs in a group born in a 3-wk interval. Animals in a group were measured on the same day. Average age per group at the start of the test varied between 65 and 100 d on both farms. The variation among groups in age at start of the test is due to variation in number of litters in each 3-wk period, because testing facilities were sometimes limiting. The duration of the test period averaged 85 d. Pigs were given ad libitum access to feed. Animals were weighed at the start and the end of the test and probed for backfat (10th rib) at the end of the test. Backfat depth measured on animal i was adjusted for body weight at probing, to a body weight of 104.4 kg, with the following formula:

$$BF_{104.4;i} = BF_i + b_i * (104.4 - WT_i), \qquad [1]$$

where b_i is estimated as:

$$\hat{b}_i = \frac{BF_i}{(WT_i - 17.3)}. \qquad [2]$$

For this method it is assumed that all individual regression lines have one point in common, namely the point on an over-all regression line at which backfat depth is zero, and body weight is estimated to be 17.3. The method supposedly preserves genetic variation in b_i.

The estimated breeding values for daily gain in the test, backfat adjusted for body weight, number liveborn, and litter weaning weight were combined in an index. Both farms used the same index.

Gilts were kept in the finishing house for 3 to 4 wk after completing the performance test and then moved to the breeding area. Once in the breeding unit, they were observed daily for signs of estrus. They were mated at either the second or third estrus, which was between 6.5 and 8 mo of age. Hormonal treatment was not applied to induce puberty or to induce estrus after weaning. Before breeding, gilts were fed 2.2 to 2.5 kg/d. During standing heat they were fed 1.5 kg/d. After breeding, gilts were moved to gestation crates and fed 2 to 2.5 kg/d, depending on condition. After 30 to 40 d, gilts were moved to gestation pens, in groups of no more than 10 gilts and sows, according to condition. Those considered to be thin were fed 2.5 to 3 kg/d. Gilts and sows were moved into farrowing crates at 110 d of gestation and fed 3 kg/d until farrowing. After farrowing, all females were given three meals of 1 kg of feed per meal for 1 d and then given all the feed they would consume throughout lactation. Normal intakes ranged from 3 to 9 kg/d.

Crossfostering was done shortly after farrowing. Piglets were weaned after a 3-wk suckling period. After weaning, sows were given 2 to 3 kg/d, depending on condition. The diet fed was a corn-soybean diet with approximately 15% crude protein and 3200 kcal/kg.

Sows were mated on their first estrus following weaning. Sows were usually culled if they returned to estrus following the second postweaning mating. Sows that aborted, and sows that lost their entire litter shortly after farrowing were usually culled immediately. Sows not in estrus by 25 d after weaning were also usually culled.

Traits recorded were farrowing date, total number of piglets born, piglets born alive, litter size after crossfostering, length of the suckling period, and litter weaning weight. Age at farrowing and the interval from weaning to farrowing were calculated from these records.

Analysis of intervals from weaning to farrowing. Phenotypic distributions of the interval from weaning to farrowing were analyzed using a Maximum Likelihood algorithm, based on the algorithm of Agha and Ibrahim (1984), to estimate parameters of the following mixture of a normal (h) and an exponential distribution (g):

$$f(x) = p * h(x; \mu_N, \sigma_N) + (1 - p) * g(x; \mu_e, s) \qquad [3]$$

where f(x) is the probability that an interval from weaning to farrowing of x days is observed; and

$$h(x;\mu_N,\sigma_N)=\frac{1}{\sqrt{(2*\pi)}*\sigma_N}*e^{-\frac{1}{2}*\left(\frac{x-\mu_N}{\sigma_N}\right)^2} \qquad [4]$$

and

$$g(x;\mu_e,s)=\left(\frac{1}{\mu_e}\right)*e^{-\left(\frac{x-s}{\mu_e}\right)},\ x\ \geq\ s \qquad [5]$$

$$g(x;\mu_e,s)=0,\ x\ <\ s \qquad [6]$$

The normal distribution represents normal intervals, and the exponential distribution is for prolonged intervals. Hence, the relative contribution, p, is the incidence of normal intervals. Subsets of farm, breed, and parity were too small to estimate all parameters in each subset. Therefore, parameters were estimated across breeds within parities, across parities within breeds, and in the entire set. To estimate the relative contribution of the underlying distributions (p) in the small subsets of farm, breed and parity, the other parameters (μ_N, σ_N, μ_e, and s) were held constant at the estimates derived from the entire set of data. The parameters μ_N and σ_N are the mean and standard deviation, respectively, of the normal distribution, μ_e and s are the mean and starting point, respectively of the exponential distribution.

Estimates for each subset were used to transform an observed interval from weaning to farrowing of x days to the probability q_x that the observed interval came from the exponential part of the distribution.

$$q_x=\frac{(1-p)*g(x;\mu_e,s)}{f(x)} \qquad [7]$$

For most intervals from weaning to farrowing, q_x has a value of 0 or 1, but for some intervals (i.e. where the two distributions overlap) q_x has a value between 0 and 1.

Models. The following linear model was used to estimate variance and covariance components of test traits:

$$y = X\beta + Wt + Zu + e \quad [8]$$

where **y** is the vector of observations for all the traits in the analysis; **β**, **t**, **u**, and **e** are vectors of fixed, litter, animal, and residual effects; and **X**, **W**, and **Z** are known design matrices. Expectations and variances of random variables were

$$E\begin{bmatrix} t \\ u \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}; \; V\begin{bmatrix} t \\ u \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{D_0} \otimes \mathbf{I} & 0 & 0 \\ 0 & \mathbf{G_0} \otimes \mathbf{A} & 0 \\ 0 & 0 & \mathbf{R_0} \otimes \mathbf{I} \end{bmatrix} \quad [9]$$

where ⊗ denotes a direct product operation; $\mathbf{D_0}$, $\mathbf{G_0}$, and $\mathbf{R_0}$ are common-environmental, genetic, and residual covariance matrices, with order equal to the number of traits in the analysis; and **A** is the numerator relationship matrix. Fixed effects were contemporary group, breed, and sex for each of the test traits. In addition, age at start of the test, age at end of the test, and body weight at the end of the test were used as covariates for weight at start of the test, weight at end of the test, and backfat at end of the test, respectively.

Interval from weaning to farrowing was analyzed within parities, using a model similar to Equation [8], except for the common environmental effects. Fixed effects were breed and farrowing group (6 groups/yr).

Initial analyses showed that genetic parameters were similar across breeds within farms, so datasets of breeds were combined within herds. Including only data from sows with an observed interval from weaning to estrus means the data is a set of censored data, because sows culled for anestrus are not included. It was not recorded which sows were culled for anestrus, so we assumed that sows that were culled after completing a lactation normally (normal lactation period, not a small litter) were culled for anestrus, which of course is not entirely correct either. Data from these sows were added to the first set to create a second set.

A derivative-free REML algorithm, as applied in the MTDFREML programs (Boldman et al., 1993), was used to estimate components of variance. Solutions for fixed effects and estimated breeding values were obtained from these analyses when convergence was reached.

Phenotypic means for reproduction traits and test traits were estimated ignoring common-environmental and animal effects (GENSTAT, 1993). Differences between means were tested using a two-tailed t-test, and differences in incidence were tested using Fisher's exact test.

Estimation of linear contrasts. After estimating breeding values ($\hat{\mathbf{u}}$), differences between the means of estimated breeding values for test traits of sows with a normal and a prolonged interval were estimated as a linear contrast of estimated breeding values, $\mathbf{k}'\hat{\mathbf{u}}$, to be able to calculate the variance of the difference. Using $\mathbf{k}'\hat{\mathbf{u}}$ to calculate the contrast, the variance of the contrast becomes

$$V(\mathbf{k}'\hat{\mathbf{u}}) = \mathbf{k}'\mathbf{A}\sigma_u^2\mathbf{k} - \mathbf{k}'\mathbf{C}^{22}\mathbf{k} \qquad [10]$$

where $\mathbf{C}^{22}$ is the animal by animal part of the inverse coefficient matrix from the mixed model equations used to estimate breeding values (Kennedy, 1990); and $\mathbf{k}$ is defined by

$$\mathbf{k}'\hat{\mathbf{u}} = \hat{\mu}_p - \hat{\mu}_n = \begin{bmatrix} -1 & 1 \end{bmatrix} \begin{bmatrix} \mathbf{x}_n'\mathbf{x}_n & \mathbf{x}_n'\mathbf{x}_n \\ \mathbf{x}_n'\mathbf{x}_n & \mathbf{x}_n'\mathbf{x}_n \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{x}_n' \\ \mathbf{x}_p' \end{bmatrix} \hat{\mathrm{u}} \qquad [11]$$

where $\mathbf{x}_p$ is a vector of transformed intervals from weaning to farrowing, q, from Equation [7], and $\mathbf{x}_n$ is a vector of (1-q). Essentially, $\mathbf{x}_n$ and $\mathbf{x}_p$ are incidence vectors of normal intervals and prolonged intervals. A least-squares method as applied in [7] is needed to estimate the average of the estimated breeding values of sows with a normal interval ($\hat{\mathbf{u}}_n$) and a prolonged interval from weaning to farrowing ($\hat{\mathbf{u}}_p$). This is because not all intervals could be classified as either normal or prolonged, but a probability of being a prolonged interval was assigned to it instead. Hence, $\mathbf{x}_n'\mathbf{x}_p$ does not equal 0. If an animal did not have an observed interval, corresponding elements in $\mathbf{x}_p$ and $\mathbf{x}_n$ were set to zero. Linear contrasts were estimated in the set without data from culled sows and in the set including data from culled sows.

Estimation of genetic trend. Genetic trend was obtained by regressing estimated breeding values of tested animals on sequentially numbered periods of 6 mo. Animals were assigned to a period based on the contemporary group in which they were tested. Regression was performed by estimating a linear contrast of estimated breeding values **k'û** with variance equal to [10]; and **k** is defined by

$$\mathbf{k}'\hat{\mathbf{u}} = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} a \\ b \end{bmatrix} = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} \mathbf{x}_1'\mathbf{x}_1 & \mathbf{x}_1'\mathbf{x}_2 \\ \mathbf{x}_2'\mathbf{x}_1 & \mathbf{x}_2'\mathbf{x}_2 \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{x}_1' \\ \mathbf{x}_2' \end{bmatrix} \hat{\mathbf{u}} \qquad [12]$$

where $\mathbf{x}_1$ is a vector with ones for tested animals and zero otherwise, and $\mathbf{x}_2$ is vector with the sequential period number for a tested animal and zero otherwise; a is the intercept and b the coefficient of regression of estimated breeding values on the period numbers.

Estimation of environmental trend. Environmental trend was estimated by regression of solutions for contemporary-group effects on sequentially numbered periods of 6 mo, weighted by the number of animals tested in the contemporary group, using the linear contrast $\mathbf{k}'_i$, with variance

$$V(\mathbf{k}'\hat{\beta}_i) = \mathbf{k}'\mathbf{C}^{11i}\mathbf{k} \qquad [13]$$

where $\mathbf{C}^{11i}$ is the contemporary group by contemporary group part of the inverse coefficient matrix from the mixed model equations; and k is defined by

$$\mathbf{k}'\hat{\beta}_i = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} a \\ b \end{bmatrix} = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} \mathbf{x}_3'\mathbf{W}\mathbf{x}_3 & \mathbf{x}_3'\mathbf{W}\mathbf{x}_4 \\ \mathbf{x}_4'\mathbf{W}\mathbf{x}_3 & \mathbf{x}_4'\mathbf{W}\mathbf{x}_4 \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{x}_3'\mathbf{W} \\ \mathbf{x}_4'\mathbf{W} \end{bmatrix} \hat{\beta}_i \qquad [14]$$

where $_i$ is the part of that corresponds with the solutions for the contemporary group effects; $\mathbf{x}_3$ is a vector of ones; $\mathbf{x}_4$ is a vector of period numbers assigned to the contemporary groups; and **W** is a matrix with the number of tested animals per contemporary group on the diagonal, and zero otherwise.

Phenotypic trends in incidence of prolonged intervals from weaning to farrowing were estimated by a linear regression of incidence in a 6-mo period on the period number.

Table 1. Phenotypic means of reproduction traits for Large White (LW) and Landrace (LR) sows of parity 1, 2, and 3 on farm 1 and 2.

		Parity 1		Parity 2		Parity 3	
Trait	σ_p	LW	LR	LW	LR	LW	LR
Farm 1							
No. of farrowings		676	311	438	220	370	169
Age at first farrowing, d	44.7	368^a	363^a				
No. piglets born alive	2.8	8.18^a	8.64^b	9.09^a	9.29^a	9.71^a	9.59^a
No. piglets weaned	2.1	8.65^a	8.84^a	8.86^a	9.12^a	9.20^a	9.35^a
Litter weaning weight, kg	12.3	44.9^a	48.4^b	50.5^a	54.4^b	52.4^a	56.1^b
No. culled, %		38.6^a	34.1^a	33.6^a	36.8^a	36.5^a	31.4^a
No. observed intervals		410	202	290	136	235	115
Interval weaning to farrowing, d	27.6	135.2^a	141.5^b	130.2^a	130.9^a	127.3^a	131.4^a
Incidence of normal intervals, %		56.4^a	26.6^b	66.8^a	60.0^a	77.1^a	65.5^b
Farm 2							
No. of farrowings		585	350	421	214	304	141
Age at first farrowing, d	30.2	345^a	350^b				
No. piglets born alive	2.7	8.72^a	9.22^b	8.87^a	9.12^a	9.55^a	9.59^a
No. piglets weaned	1.9	8.95^a	9.23^b	9.06^a	9.28^a	8.97^a	9.34^b
Litter weaning weight, kg	11.7	47.6^a	52.6^b	52.1^a	57.7^b	52.7^a	57.3^b
No. culled, %		31.1^a	39.7^b	28.3^a	34.6^a	33.6^a	34.8^a
No. observed intervals		402	211	302	140	202	92
Interval weaning to farrowing, d	23.2	128.9^a	135.6^b	128.0^a	130.1^a	126.3^a	136.5^b
Incidence of normal intervals, %		68.9^a	35.9^b	77.4^a	55.3^b	80.0^a	67.6^b

^{a,b}Means within a row within a parity with differing subscript differ ($P < .05$)

Results

Analysis of intervals from weaning to farrowing. Landrace sows had longer average intervals from weaning to farrowing after the first parity on each farm and after the third parity

Table 2. Parameter estimates of a mixture of a normal and an exponential distribution in subsets of data.

Trait	N[a]	p	μ_N	σ_N	μ_e	s	Type[b]
Farm 1							
Parity 1	612	.52	122.6	2.3	34.6	119	F
Parity 2	426	.65	121.8	2.1	32.8	120	F
Large White	1077	.70	122.0	2.4	36.3	120	F
Landrace	507	.48	121.8	2.0	29.4	119	F
Farm 2							
Parity 1	613	.60	122.6	2.7	26.9	119	F
Parity 2	442	.72	122.0	2.6	28.5	119	F
Large White	1105	.76	121.8	2.5	31.0	119	F
Landrace	554	.52	122.2	2.4	24.7	120	F
Farm 1 and 2	3243	.63	121.9	2.4	28.8	119	F
Ten Napel et al., 1995b							
Selection line	1115	.39	5.6	1.1	36.8	5	E
Control line	1018	.31	5.6	1.0	36.9	5	E
Dutch commercial herds (Ten Napel et al., 1995a)							
Parity 1	57800	.56	5.4	1.2	21.1	5	M
Parity 2	43845	.80	5.4	1.1	18.8	5	M
Parity 3 and higher	130261	.90	5.4	1.1	18.8	5	M
Fahmy et al., 1979	549	.17	5.7	1.4	21.5	5	E

[a] Abbreviations: N = number of intervals in the analysis; p = incidence of normal intervals; μ_N, σ_N = mean and standard deviation of the normal distribution; μ_e, s = mean and starting day of exponential distribution
[b] Type of interval analysed: E=interval from weaning to estrus; M=interval from weaning to mating; F=interval from weaning to farrowing

on farm 2 (Table 1). Incidence of normal intervals was least in Parity 1 in each breed on both farms, and was less in Landrace than Large White sows (Table 1).

Phenotypic distributions of intervals from weaning to farrowing of different subsets of data were very similar, with a major peak at d 121 and a minor peak 3 wk later, and a tail up to d 300, as is shown in Figure 1 for Landrace and Large White sows on Farm 1. Distributions of intervals observed on Farm 2 were similar. Parameters of the underlying distributions estimated within parities across breeds, within breeds across parities, and in the entire set of

Table 3. Phenotypic means of test traits for Large White (LW) and Landrace (LR) pigs on farm 1 and 2.

	Farm 1			Farm 2		
Trait	σ_p	LW	LR	σ_p	LW	LR
Number of pigs tested		10876	4865		9086	5410
Age at start of test, d	11.8	92.2^a	90.5^b	8.4	79.8^a	79.0^b
Weight at start of test, kg	8.6	33.1^a	33.9^b	5.1	28.6^a	28.7^a
Age at end of test, d	7.0	177.0^a	176.3^b	6.3	164.6^a	164.3^b
Weight at end of test, kg	13.2	100.0^a	100.6^b	10.2	94.2^a	91.8^b
Average daily gain in test, g/d	106	768^a	761^b	85	773^a	740^b
Backfat depth 10th rib, mm	4.0	12.9^a	12.5^b	3.4	12.2^a	11.6^b
Weight-adjusted backfat, mm	4.1	14.5^a	14.0^b	2.5	13.8^a	13.2^b

^{a,b}Means within a row within a farm with differing subscript differ ($P < .05$)

data were similar (Table 2), but the relative contribution was different. Relative contributions in subsets of farm, breed and parity are shown in Table 1.

Descriptive statistics. Number of pigs born alive was higher for Landrace than Large White sows of Parity 1 (Table 1). Number of pigs weaned is in some subsets higher than the number born alive, due to the routine of entirely crossfostering small litters. Litter weaning weight was higher for Landrace than Large White sows in each parity. More Landrace than Large White first-litter sows were culled after weaning on Farm 2. Landrace pigs were younger than the Large White pigs at the start and the end of the test on each farm, had a slower daily gains in the test, and lower backfat depths at the end of the test (Table 3).

Relationships with test traits. Heritabilities, proportion of variance due to common environment, and correlations among test traits were of similar magnitude on each farm (Table 4 and 5). Genetic correlations between test traits and intervals from weaning to farrowing had opposite sign on the two farms. The heritability of the interval from weaning to farrowing was zero in sows of Parity 1 on Farm 1, and Parity 3 of Farm 2.

Differences in estimated breeding values for test traits between sows with a normal and a prolonged interval were only found in Parity 1 on each farm, but the differences on the two farms had opposite sign (Table 6). After including sows which were culled after weaning the first litter as sows with a prolonged interval, differences in average estimated breeding value for daily gain and backfat were consistent across breeds and farms in Parity 1 (Table 6).

Table 4. Heritabilities, genetic correlations (above the diagonal), and phenotypic correlations (below the diagonal) of test and rebreeding traits on farm 1 and 2.

Trait	ADG	BFA	WF1	WF2	WF3
Farm 1					
Average daily gain in test (ADG)	**.23**	.19	-[a]	-.12	-.64
Backfat depth adjusted for body weight (BFA)	.13	**.49**	-[a]	-.28	-.24
Interval weaning-farrowing, 1st parity (WF1)	.06	-.02	**.00**	-[a]	-[a]
Interval weaning-farrowing, 2nd parity (WF2)	-.06	-.12	.09	**.05**	.78
Interval weaning-farrowing, 3rd parity (WF3)	-.21	-.07	-.01	.13	**.24**
Farm 2					
Average daily gain in the test (ADG)	**.32**	.13	.21	.08	-[a]
Backfat depth adjusted for body weight (BFA)	-.04	**.43**	.21	.18	-[a]
Interval weaning-farrowing, 1st parity (WF1)	-.05	.05	**.12**	.74	-[a]
Interval weaning-farrowing, 2nd parity (WF2)	.04	.05	.15	**.16**	-[a]
Interval weaning-farrowing, 3rd parity (WF3)	-.02	-.02	.00	.02	**.00**

[a] Could not be estimated because h^2=0

[b] Approximate standard errors of the heritabilities ranged from .03 for the test traits to .1 for the interval traits. Approximate standard errors of genetic correlations ranged from .1 to .2.

Genetic and environmental trends were significant in each breed on each farm, except for backfat depth on Farm 2 (Table 7). An unfavorable phenotypic trend in incidence of prolonged intervals was observed in first-parity sows of each of the two breeds on Farm 1, but not on Farm 2 (Table 8). Phenotypic trends in incidence of prolonged intervals were also observed in third-parity Landrace sows, but with opposite sign on the two farms (Table 8).

Discussion

Analysis of interval from weaning to farrowing. The profile of the distribution shown in Figure 1 is similar to the profile of distributions of the interval from weaning to estrus (Ten Napel et al., 1995b). The minor peaks at 3 wk after the major peaks were probably due to a regular return to estrus after a non-successful mating, rather than silent estrus.

The observation that estimated parameters of the underlying distributions were similar in different subsets of the data (Table 2), is in agreement with results of Ten Napel et al. (1995b),

Table 5. Amount of variation due to common-environmental effects (c^2), correlations between common-environmental effects (above the diagonal), and environmental correlations (below the diagonal) of test and rebreeding traits on farm 1 and 2.

Trait	ADG	BFA	WF1	WF2	WF3
Farm 1					
Average daily gain in test (ADG)	**.07**	.08	-	-	-
Backfat depth adjusted for body weight (BFA)	.11	**.06**	-	-	-
Interval weaning-farrowing, 1st parity (WF1)	.01	-.02	-	-	-
Interval weaning-farrowing, 2nd parity (WF2)	-.06	-.12	.10	-	-
Interval weaning-farrowing, 3rd parity (WF3)	-.10	-.07	.03	.06	-
Farm 2					
Average daily gain in test (ADG)	**.06**	-.22	-	-	-
Backfat depth adjusted for body weight (BFA)	-.06	**.05**	-	-	-
Interval weaning-farrowing, 1st parity (WF1)	-.12	.01	-	-	-
Interval weaning-farrowing, 2nd parity (WF2)	.03	-.01	.00	-	-
Interval weaning-farrowing, 3rd parity (WF3)	-.03	-.03	.00	.03	-

for the interval from weaning to estrus, and with analyses of data from Dutch commercial breeding herds (Ten Napel et al., 1995a), for the interval from weaning to fertile mating (Table 2). Sows on these breeding herds were all purebred sows of one breed, and herds were supposed not to use hormonal treatment to induce estrus. Estimates of the variance of the underlying normal distribution were slightly greater in data of intervals from weaning to fertile mating or farrowing, compared to estrus. Estimates of the mean of the exponential distribution varied among data sets, due to variation in culling policy, and were greatest when culling because of anestrus was not practised. Culling because of anestrus causes a decrease of the mean of the exponential distribution. Rebreeding sows after a non-successful mating, however, increases the mean of the exponential distribution in the case of the interval from weaning to farrowing.

In conclusion, variation in selection strategies and management procedures, except for culling, does not cause changes in the distribution of normal or prolonged intervals, but only affects the probability of having a normal or prolonged interval. This justifies the method of estimating the parameters of the underlying distributions in the entire set of data and using

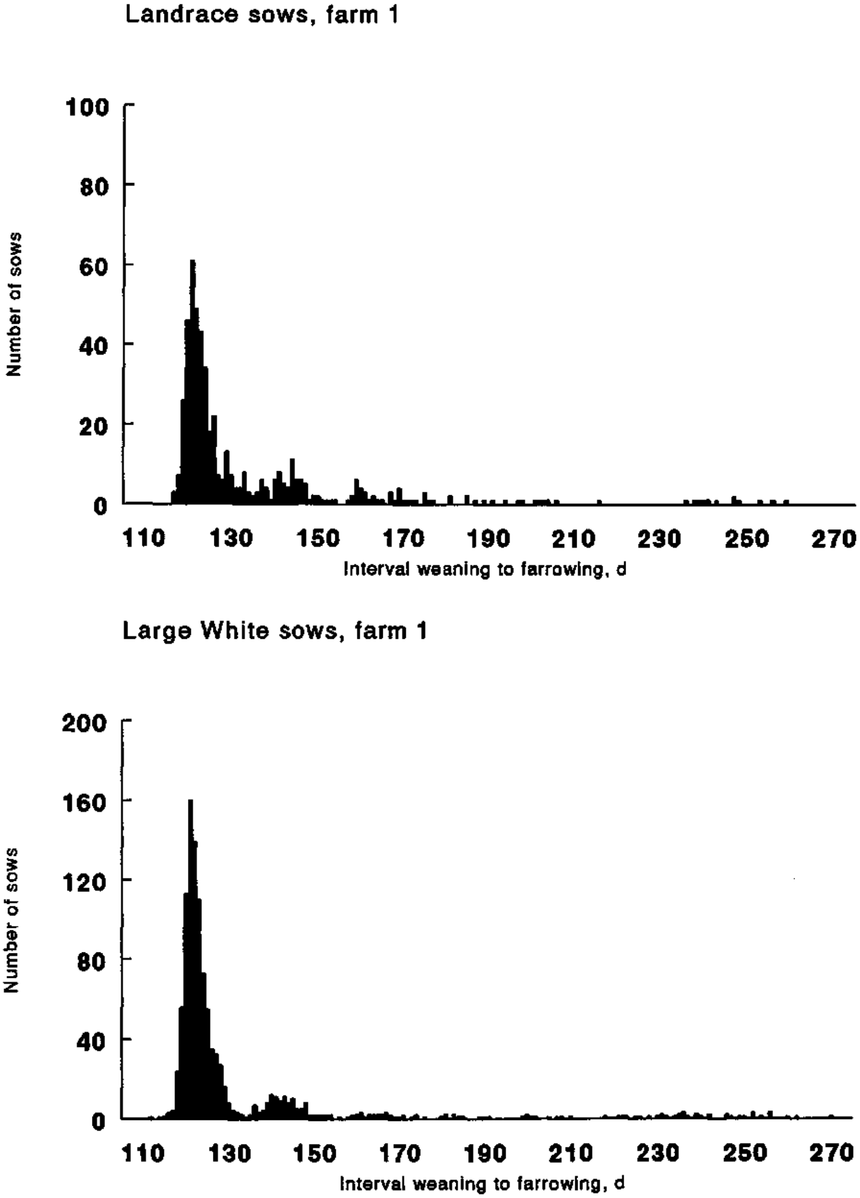

Figure 1. Interval from weaning to farrowing for Landrace sows and Large White sows at Farm 1.

these estimates to estimate the incidence of normal intervals in subsets of data that were too small to estimate all parameters at once (% normal intervals in Table 1).

Table 6. Differences in average estimated breeding value for test and reproduction traits between sows with prolonged and normal intervals from weaning to farrowing on farm 1 and 2 (prolonged minus normal)

	Parity 1		Parity 2		Parity 3		Parity 1[a]	
Trait	LW	LR	LW	LR	LW	LR	LW	LR
Farm 1								
Average daily gain in test, g/d	16.8[c]	23.1	7.3	1.0	-5.9	-0.6	14.6[c]	24.9[b]
Backfat adjusted for body weight, mm	-.52[b]	.29	-.28	-.29	-.28	-.41	-.64[c]	-.17
No. piglets born alive	.11[c]	.06	.01	.02	.03	.07	.05[c]	.02
Litter weaning weight, kg	1.00[c]	.50	.01	.44	.12	1.09	.42	.38
Farm 2								
Average daily gain in test, g/d	-13.8[c]	-6.4	4.6	4.3	-3.3	3.9	10.5[c]	28.7[c]
Backfat adjusted for body weight, mm	.30	.37	.28	.37	.39	-.19	-.00	-.28
No. piglets born alive	-.01	-.13	.00	-.03	-.05	.01	.03	-.03
Litter weaning weight, kg	.15	-.25	-.65	-.21	-.57	-.52	.57	.81

[a] Sows culled after weaning the first litter are considered having a prolonged interval

[b] Different from zero (P < .10)

[c] Different from zero (P < .05)

In distributions of intervals from weaning to estrus the overlap of the normal and the exponential distribution is small, so when intervals longer than 7 d are classified as prolonged, and otherwise normal, the amount of incorrectly classified intervals is less than 5%. Due to variation in gestation length, the overlap of the two distributions is larger in intervals from weaning to farrowing. Therefore, some intervals cannot be classified as either normal or prolonged, so instead a probability of being a prolonged interval was assigned, using Equation [7].

Relationships with test traits. In a review, Ten Napel et al. (1995a) hypothesized that genetic selection for increased daily gain, decreased backfat depth, increased litter size at birth, or increased litter weight at weaning may impair normal resumption of cyclic activity after weaning, in particular after weaning the first litter. To check this hypothesis, we would have preferred to have interval from weaning to estrus available, but date of first estrus was not

Table 7. Genetic and environmental trends for test and reproduction traits on farm 1 and 2 per 6-mo period.

	Farm 1			Farm 2		
	Genetic		Env.	Genetic		Env.
Trait	LW	LR		LW	LR	
Average daily gain in test, g/d	6.7^b	5.1^b	-7.9^b	10.2^b	7.0^b	-8.9^b
Backfat depth, adjusted for body weight, mm	-.14^b	-.20^a	-.36^b	-.04	-.06	-.20^b
No. piglets born alive	.02^b	.02^b	-.09^a	.04^b	.04^b	-.11^a
Litter weaning weight, kg	.52^b	.48^b	-.80^b	.40^b	.36^b	-.29

[a] Different from zero ($P < .05$)
[b] Different from zero ($P < .001$)

recorded in these populations, so instead we used interval from weaning to farrowing, which includes interval from weaning to estrus.

Whether (genetic) variation in rebreeding performance is observed depends on the level of management. The more extreme (favorable or unfavorable) the environment, the less variation is observed (Ten Napel et al., 1995a). Although farms were supposed to have the same management procedures, environments were slightly different across farms with respect to construction of buildings and crowding of animals. For this reason rebreeding performance was analyzed within farms. Only a few genetic links existed between the two sets of data because no animals were exchanged after the start of Farm 2.

Estimates of heritability of the interval from weaning to farrowing after the first parity were less than those reported for the interval from weaning to estrus (Ten Napel, 1995b; Petrovicova et al., 1988; Fahmy et al., 1979), and similar to those reported for the farrowing interval (Johansson and Kennedy, 1983; Maurer et al., 1985; Rydhmer et al., 1995). Apparently, additional variation due to returns to estrus after non-successful matings has only a small genetic basis. Because the heritabilities of the interval from weaning to farrowing are low, and because of the low genetic correlations with the traits under selection, genetic selection for increased daily gain and decreased backfat would be expected to only have a neglible effect on rebreeding performance.

Table 8. Phenotypic trends in a 6-mo period in incidence of a prolonged interval in 1st, 2nd, and 3rd parity Large White (LW) and Landrace (LR) sows on farm 1 and 2.

	Farm 1		Farm 2	
Trait	LW	LR	LW	LR
Incidence prolonged intervals (1st parity), %	1.47[a]	.88[a]	-.67	-1.85
Incidence prolonged intervals (2nd parity), %	.48	.26	-2.27	-.47
Incidence prolonged intervals (3rd parity), %	.20	3.65[a]	-2.94	-4.02[a]

[a] Different from zero ($P < .05$)

Heritability estimates for growth rate were higher than those reported in other studies concerning pigs tested on-farm (Merks, 1988; Hofer et al., 1992). Percentage of variation explained by common litter effects was smaller than estimated in these studies. Heritability estimates for backfat depth were higher than those reported by Merks (1988) but similar to estimates in other studies (Van Diepen and Kennedy, 1989; Long et al., 1990; McKay, 1990). Estimates of variation explained by common litter effects are lower in this study than in other studies (Merks, 1988; Van Diepen and Kennedy, 1989; Hofer et al., 1992).

To study effects of selection for improved production on rebreeding performance in an alternative way, we estimated differences in average estimated breeding values for the traits under selection between sows with normal and prolonged intervals. In terms of this method, the above hypothesis may be true when sows with a prolonged interval have on average a more favorable estimated breeding value for the traits selected for, than sows with a normal interval. When analyzing observed intervals (first dataset), the results seem inconclusive. The differences in Large White sows on Farm 1 and Farm 2 have opposite sign (Table 6). Significant differences in estimated breeding values were only observed in sows of Parity 1. When data from culled sows was included in the analysis (second set), the differences between sows with normal and prolonged intervals were as hypothesized, and were consistent across breeds and farms (Table 6), although not always significant. The results from the second set support the idea of unfavorable correlated responses in rebreeding performance due to selection for production traits.

The assumption that culled sows would have had a prolonged interval from weaning to estrus (and farrowing) seems crucial for our conclusion. Although we do not have data, we suppose that occurrence of anestrus is more frequent than returning to estrus after a non-successful mating twice in a row, abortion or disease. Further, we expected that these conditions would not have a strong genetic relationship with the traits under selection. Thus, incorrectly assuming that these sows would have had a prolonged interval would decrease the estimated contrast rather than create a non-existent contrast.

When we analysed linear contrasts and genetic and environmental trends, we used solutions from the one analysis (estimated breeding values, solutions for effects of season) as dependent variables in another. This was done under the assumptions that the model used for estimating breeding values was correct, and the components of variance were known. The procedure for testing linear contrasts and trends accounted for covariances between estimated breeding values and differences in precision.

Estimated breeding values were compared using a phenotypic classification of intervals to normal and prolonged intervals. A situation cannot be envisioned where environmental factors may have caused the consistent differences found. Therefore, the relationship between the production traits and rebreeding performance has a genetic basis.

Sows with an interval from weaning to farrowing longer than about 140 d are likely to have returned to estrus after not conceiving from the first mating, because anestrous sows were generally culled at 25 d postweaning. The number of intervals longer than 140 d was substantial (Figure 1 and 2). The absence of consistent contrasts in estimated breeding values in the first dataset suggests that not-conceiving after mating is not related to the traits under selection.

The contrast for the reproduction traits increased after culling on Farm 1, but not on Farm 2. Apparently a delayed estrus was acceptable on Farm 1 if the sow had extremely good mothering abilities. This difference in culling policy may be the reason an unfavorable phenotypic trend in incidence of prolonged intervals was observed on Farm 1 and not on Farm 2, because genetic trends for production traits on the two farms were similar. However, the observed trend in incidence of prolonged intervals may be a poor estimation of the true trend because sows culled for anestrus were not taken into account.

Genetic correlations between test traits and interval from weaning to farrowing may not be useful for predicting correlated responses in rebreeding performance to selection for production because the fact that normal and prolonged intervals can be distinguished is ignored. In fact, these genetic correlations are some kind of pooling of the genetic correlations of test traits with normal intervals, prolonged intervals, and the probability of a normal interval. The distributions of normal intervals and prolonged intervals are similar in independent populations (Table 2), and response to selection for a short interval from weaning to estrus was an increase in incidence of normal intervals (Ten Napel et al., 1995b), rather than a change of the distributions of normal or prolonged intervals. Therefore, the genetic correlations between test traits and the length of normal intervals, or the length of prolonged intervals are probably low. The genetic correlations between test traits and the probability of a normal interval are probably greater than correlations with the length of the interval, but unbiased estimates of such a correlation are difficult to obtain.

In conclusion, analysis of the interval from weaning to farrowing as a continuous trait yielded low estimates for genetic parameters, which would indicate that genetic selection for production and reproduction traits does not affect rebreeding performance. However, when the trait was transformed to the probability of being a prolonged interval, and data from culled animals were used, relationships were such that genetic selection for increased daily gain and for decreased backfat to a lesser extent would increase the probability of a prolonged interval from weaning to farrowing.

Implications

It is possible and advantageous to classify rebreeding intervals into normal and prolonged intervals. If sows culled because of anestrus are likely to have had a prolonged interval, they can also be included in the analysis. The classification of normal and prolonged intervals and the inclusion of sows culled for anestrus may be helpful for the analysis of physiological and endocrinological studies in the postweaning sow to achieve a maximal contrast. If an unfavourable genetic relationship between traits under selection and rebreeding performance exists, then breeding herds probably should not use any kind of hormonal treatment to induce estrus after weaning to avoid a correlated increase in incidence of prolonged intervals to selection for growth, backfat, and litter size, and weight.

Acknowledgement

We acknowledge National Genetic Technology (Columbus, NE) for providing the sets of data. We also wish to thank E. W. Brascamp, B. Kemp, T.H.E. Meuwissen, and A. G. de Vries for discussion and reading of the manuscript.

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Chapter 5

Genetics of Interval from Weaning to Estrus in First-Litter Sows. II. Correlated Responses on Breeding Traits

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Submitted for publication in Journal of Animal Science.

Abstract

Correlated responses of sow and litter traits to selection for a short interval from weaning to estrus were studied using data of 2242 Dutch Landrace sows by estimating phenotypic and genetic trends across eight generations. Estimated relationships between breeding traits and rebreeding performance were phenotypic, genetic and residual correlations with interval from weaning to estrus, length of normal intervals, and length of prolonged intervals. Relationships between a trait and incidence of a prolonged interval were estimated by evaluating the difference in average EBV for that trait between sows with a normal interval and sows with a prolonged interval. Principal components were derived from the entire set of breeding traits, and those accounting for 10% or more of the variation were analyzed as new traits. No genetic trend or phenotypic trend for breeding traits or principal components was found. Heritabilities of normal intervals, prolonged intervals and incidence of prolonged intervals were .18, .17 and .27. Daily gain in litter weight as a measure of milk production, and loss of body condition during lactation were positively genetically correlated with the length of normal intervals, but negatively with the length of prolonged intervals. Average EBV for daily gain in litter weight, body condition at weaning and the first principal component, interpreted as a measure of sow productivity, were different between sows with a normal and sows with a prolonged interval in both lines. Other traits were different in only one line. The procedure of selecting selection-line gilts as a dam only if not treated with hormones to induce puberty, interfered with selection. It was concluded that the selection applied did not cause a measurable correlated response in any of the breeding traits, but there is evidence that selection for improved sow productivity may increase incidence of prolonged intervals.

Key words: Rebreeding, Selection, Correlated response, Litter performance, Condition score

Introduction

Performance during lactation determines to a large extent whether the sow will have a normal return to estrus. Severe losses of body weight and (or) backfat increase the time till the first estrus after weaning, especially in primiparous sows (Reese et al., 1982a,b; Brendemuhl et al., 1987, 1989). These losses of body tissue can be due to a low feed intake during lactation or a high total milk production. A given loss of body tissue may become harmful sooner if body reserves are low at farrowing, or if the sow needs substantial amounts of nutrients for its own growth at the time of lactation (King and Williams, 1984; Mullan and Williams, 1989; Ten Napel et al., 1995a).

There is evidence that normal and prolonged intervals from weaning to estrus can be considered separate traits, such that if a normal interval was observed, the prolonged interval was not expressed, and the reverse (Ten Napel et al., 1995a; Ten Napel and Johnson, 1995). Thus, variation in interval from weaning to estrus is determined by variation in three traits, namely incidence of prolonged intervals, length of normal interval, and length of prolonged interval.

In a selection experiment for a short interval from weaning to estrus it was found that genetic selection was effective in reducing the average interval from weaning to estrus, and this reduction was achieved by decreasing the incidence of prolonged intervals, rather than changing the mean of normal intervals, or the mean of prolonged intervals (Ten Napel et al., 1995b).

In this study phenotypic and genetic trends in breeding traits due to selection for a short interval from weaning to estrus are analysed, and genetic relationships between breeding traits and rebreeding performance are studied. In addition to genetic correlations with intervals from weaning to estrus (ignoring the distinction between normal and prolonged intervals), genetic correlations of breeding traits with normal intervals, and prolonged intervals are estimated. Because some crucial assumptions are violated in the estimation of genetic correlations with incidence of prolonged intervals using a linear model, these relationships are studied by estimating the difference in average estimated breeding value for each of the breeding traits between sows with a normal return to estrus, and sows with a delayed return to estrus.

Phenotypic contrasts between these two groups are estimated to study whether prolonged intervals had similar causes as in other studies. Finally, the consequences of treating part of gilts with hormones to induce puberty are discussed.

Material and Methods

General. Data were available from a selection experiment with Dutch Landrace pigs, in which two lines were maintained. One line was selected for a short interval from weaning to estrus, and in the other line selection was avoided. The experiment started with a foundation population of purchased animals (generation 0), followed by 7 generations of intense selection (generation 1 to 7) and one generation of relaxed selection (generation 8). Selection and management procedures were described in Ten Napel et al. (1995b).

Traits recorded were body condition score of sows when they entered the farrowing unit, number of piglets born and born alive, number of piglets crossfostered, number of piglets weaned, individual piglet weights at birth and weaning, and body condition score at weaning. Traits calculated from these measurements were number of piglets that died during lactation, loss in body condition during lactation, and daily gain in litter weight during lactation. The latter is calculated by cumulating the difference between weaning weight and birth weight for suckling piglets weaned and dividing this sum by the lactation length. Loss of body condition was calculated as body condition score at farrowing minus body condition score at weaning. Body condition was visually scored on an eleven class scale, ranging from 0 to 5 with steps of .5, where 0 denotes an extremely poor body condition, and 5 a thick layer of fat.

The experimental design involved a mating period of strictly 4 wk for gilts in each mating group (Ten Napel et al., 1995b). Gilts that were not seen in estrus after 3 wk in the mating period were treated with 400 IU of PMSG + 200 IU of hCG intramuscularly. In the selection line no progeny of treated gilts was maintained for replacement, but this procedure was not practised in the control line.

Phenotypic trends. Phenotypic least-squares means of the traits measured were estimated with the REML procedure in Genstat (Genstat 5 Committee, 1993), using a model including line-generation and mating group within line-generation as fixed effects. Differences in incidence of treatment to induce puberty were tested using a X^2 test.

Phenotypic contrasts. Phenotypic contrasts between sows with a normal interval from weaning to estrus and sows with a delayed interval were studied using a principal component analysis. This is a multivariate technique to transform a number of correlated measurement variables to a set of statistically independent linear combinations of the original measurements. The first step is to estimate the phenotypic covariance matrix, after standardizing the measurement variables to a mean equal to zero and a variance equal to one. The second step is to calculate the eigenvalues and corresponding eigenvectors of the covariance matrix. The eigenvectors contain the coefficients of the linear combinations of the original standardized measurements. These linear combinations are the principal components. The first principal component is that linear combination which accounts for the highest amount of the total variation, and is calculated from the eigenvector corresponding to the largest eigenvalue (Brown et al., 1973; Young et al., 1977). Principal components thus obtained were analyzed as new traits.

The analysis requires that all variables are measured on a sow for her data to be included. Numbers of sows in this analysis are therefore lower than in other analyses in this paper (1026 sows from the selection line, and 945 from the control line). Interval from weaning to estrus was not included in the principal component analysis.

The principal component analysis was done using PROC PRINCOMP in the SAS statistical package (SAS, 1985). Phenotypic contrasts for the principal components were estimated using PROC GLM by fitting a fixed effect indicating whether the interval from weaning to estrus was normal (0) or prolonged (1).

Genetic parameters. The general model for estimating components of variance and covariance was as follows: $\mathbf{Y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$, where $\mathbf{Y}$ is a vector of observations, $\mathbf{X}$, and $\mathbf{Z}$ are known design matrices for fixed effects ($\mathbf{b}$), and genetic effects ($\mathbf{u}$), and $\mathbf{e}$ is a vector of residuals. Fixed effect was the combination of generation and mating group. Sow was included as an animal genetic effect, with $\text{var}(\mathbf{u})=\mathbf{A}\sigma$. The covariance structure of residuals was $\text{var}(\mathbf{e})=\mathbf{I}\sigma$. Covariances between $\mathbf{u}$, and $\mathbf{e}$ were assumed zero. Interval from weaning to estrus, which is the trait under selection, was not included in the analyses.

A derivative-free REML algorithm, as applied in the MTDFREML programs (Boldman et al., 1993), was used to estimate components of variance. Estimated breeding values were obtained from these analyses after the convergence criterion for variance component estimation was met.

The trait normal interval was defined as the interval from weaning to estrus if it was 7 d or shorter, and otherwise undefined (missing). Prolonged interval was defined as the interval from weaning to estrus if the interval was longer than 7 d, and otherwise undefined. So if the normal interval was observed, the prolonged interval was missing, and the reverse.

Components of variance for binary traits were estimated using a threshold animal model. The approach followed is described by Knuiman and Laird (1990). Covariances between a binary trait and a continuous trait could not be estimated with this method (using the algorithm for a sire model, described by Janss and Foulley, 1994), because convergence could not be obtained.

Numbers of sows that were included in these analyses were 1165 and 1077, for the selection and the control line, respectively.

Genetic trends. Genetic trend was obtained by regressing estimated breeding values of sows on generation number. Let a be the intercept and b the coefficient of regression of estimated breeding values on generation numbers, then

$$\begin{bmatrix} a \\ b \end{bmatrix} = \begin{bmatrix} x_1'x_1 & x_1'x_2 \\ x_2'x_1 & x_2'x_2 \end{bmatrix}^{-1} \begin{bmatrix} \mathrm{x}_1' \\ \mathrm{x}_2' \end{bmatrix} \hat{\mathrm{u}} \qquad [1]$$

where $\mathbf{x}_1$ is a vector with ones for sows with a record for the trait analysed and zero otherwise ($\mathbf{x}_1'\mathbf{x}_1$ is the total number of observations), and $\mathbf{x}_2$ is a vector with the generation number for a sow with a measurement and zero otherwise. Estimation of the standard error of b is not straightforward, because variances of estimated breeding values differ, and covariances between estimated breeding values exist. We rewrite estimation of b such that it is a linear contrast of estimated breeding values $\mathrm{k}'\hat{\mathrm{u}}$ with

$$V(\mathrm{k}'\hat{\mathrm{u}}) = \mathrm{k}'\mathrm{A}\sigma_u^2\mathrm{k} - \mathrm{k}'\mathrm{C}^{22}\mathrm{k}$$

[2]

where $\mathbf{C}^{22}$ is the animal by animal part of the inverse coefficient matrix from the mixed model equations used to estimate breeding values, and **A** is the numerator relationship matrix. We can write **k** as

$$\mathrm{k}'\hat{\mathrm{u}} = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} a \\ b \end{bmatrix} = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} \mathrm{x}_1'\mathrm{x}_1 & \mathrm{x}_1'\mathrm{x}_2 \\ \mathrm{x}_2'\mathrm{x}_1 & x_2'\mathrm{x}_2 \end{bmatrix}^{-1} \begin{bmatrix} \mathrm{x}_1' \\ x_2' \end{bmatrix} \hat{\mathrm{u}}$$

[3]

Environmental trends. Environmental trend was estimated by regression of solutions for generation-mating group effects on generation number, weighted by the number of sows with an observation in the subclass of generation and mating group, again written as a linear contrast $\mathbf{k}'\beta_i$, with variance

$$V(\mathrm{k}'\hat{\beta}_i) = \mathrm{k}'\mathrm{C}^{11i}\mathrm{k}$$

[4]

where $\mathbf{C}^{11i}$ is the generation-mating group by generation-mating group part of the inverse coefficient matrix from the mixed model equations; and $\mathbf{k}'\beta$ is defined by

$$\mathrm{k}'\hat{\beta}_i = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} a \\ b \end{bmatrix} = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} \mathrm{x}_3'\mathrm{W}\mathrm{x}_3 & \mathrm{x}_3'\mathrm{W}\mathrm{x}_4 \\ \mathrm{x}_4'\mathrm{W}\mathrm{x}_3 & \mathrm{x}_4'\mathrm{W}\mathrm{x}_4 \end{bmatrix}^{-1} \begin{bmatrix} \mathrm{x}_3'\mathrm{W} \\ \mathrm{x}_4'\mathrm{W} \end{bmatrix} \hat{\beta}_i$$

[5]

where $_i$ is the part of that corresponds with the solutions for the generation-mating group effects; $\mathbf{x}_3$ is a vector of ones; $\mathbf{x}_4$ is a vector of generation numbers assigned to the subclass of generation and mating group; and **W** is a matrix with the number of animals with an observation per subclass on the diagonal, and zero otherwise.

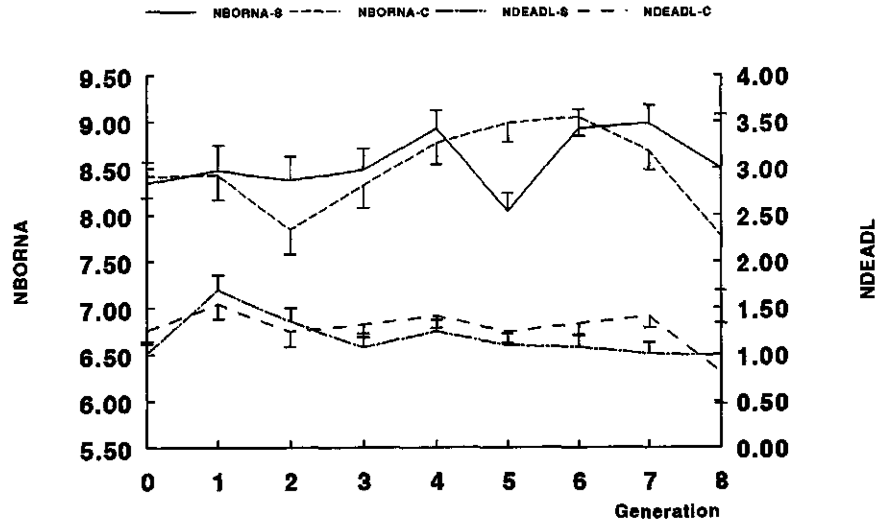

Figure 1. Number of piglets born alive (NBORNA), and number of deaths during lactation (NDEADL) per generation for the selection line (S) and the control line (C).

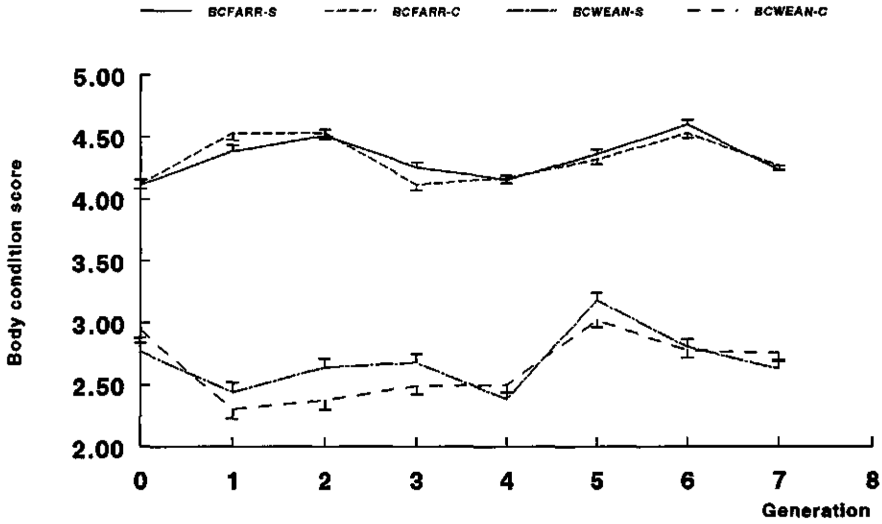

Figure 2. Body condition score at farrowing (BCFARR) and weaning (BCWEAN) per generation for the selection line (S) and the control line (C).

Genetic contrasts. Differences in estimated breeding values for rearing traits and principal components between sows with a normal and a prolonged interval were estimated as a linear contrast of estimated breeding values **k'û** with variance equal to [2]; and k is defined by

$$\mathrm{k}'\hat{\mathrm{u}} = \begin{bmatrix} -1 & 1 \end{bmatrix} \begin{bmatrix} \bar{u}_n \\ \bar{u}_p \end{bmatrix} = \begin{bmatrix} -1 & 1 \end{bmatrix} \begin{bmatrix} \mathrm{x}_n'\mathrm{x}_n & 0 \\ 0 & \mathrm{x}_p'\mathrm{x}_p \end{bmatrix}^{-1} \begin{bmatrix} \mathrm{x}_n' \\ \mathrm{x}_p' \end{bmatrix} \hat{\mathrm{u}} \qquad [6]$$

where $\mathbf{x}_p$ is a vector with elements equal to 0 if the interval from weaning to estrus was 7 d or shorter, and 1 if the interval was longer than 7 d, and $\mathbf{x}_n$ is a vector with elements equal to 1 if the interval from weaning to estrus was 7 d or shorter, and 0 if the interval was longer than 7 d. In fact, $\mathbf{x}_p$ indicates whether the observed interval was a prolonged interval, and $\mathbf{x}_n$ whether the interval was a normal interval. If an animal did not have an observed interval, corresponding elements in $\mathbf{x}_p$ and $\mathbf{x}_n$ were set to zero.

Results

Phenotypic trends. Number of piglets born alive was lower ($P < .05$) in the selection line than in the control line in generation 5 (Figure 1). Number of piglets that died during lactation was lower in the selection line than in the control line in generation 7 (Figure 1). Body condition score at farrowing was lower ($P < .05$) in the control line than in the selection line in generation 3 (Figure 2). Body condition score at weaning was higher ($P < .05$) in the control line in generation 0, but lower ($P < .05$) in generation 2 and 3 (Figure 2). Daily gain in litter weight was higher ($P < .05$) in the selection line than in the control line in generation 0, 4, and 7 (Figure 3). None of these traits showed diverging phenotypic trends due to the selection applied.

Figure 4 shows that no clear trend in incidence of induction of puberty was present in the control line, but in the selection line the use of hormonal treatments decreased over generations, most likely due to the procedure of not selecting females with induced puberty in the selection line.

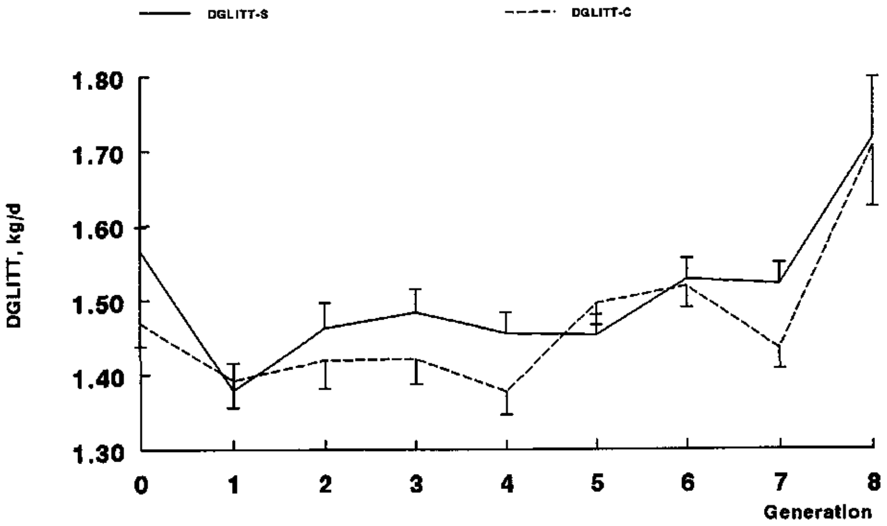

Figure 3. Average daily gain of entire litter (DGLITT) per generation for the selection line (S) and the control line (C).

Phenotypic contrasts. Figure 5 shows that both in the selection and the control line, the probability of being culled is higher for gilts treated to induce puberty, than for untreated gilts. Further, the probability of having a normal interval given an observed interval is lower for treated gilts than untreated gilts ($P < .05$).

Phenotypic contrasts between sows with a normal interval and sows with a prolonged interval were calculated using the principal components that each accounted for at least 10% of the variance. The magnitude and sign of the coefficients in the eigenvector of a particular principal component determine the importance and grouping of the original traits within that component. Within a component, traits that are weighted by large coefficients are more important than those weighted with small coefficients (Brown et al., 1973; Young et al., 1977).

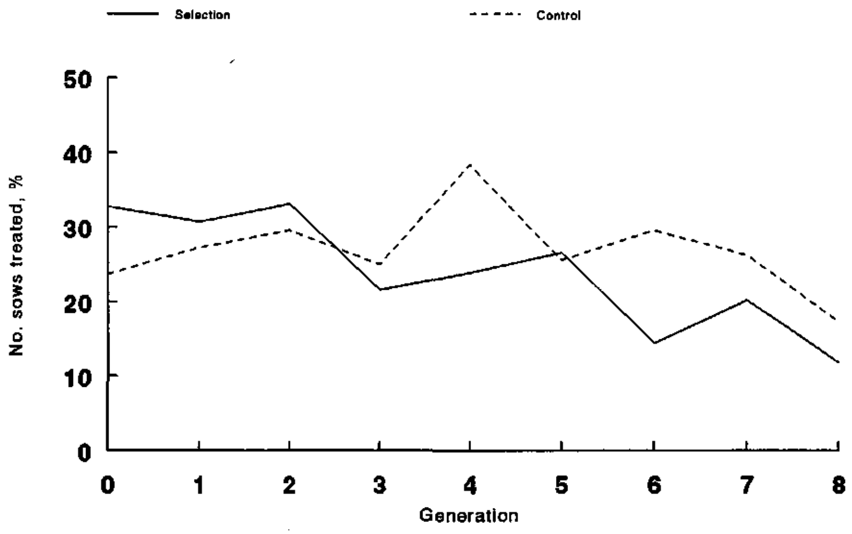

Figure 4. Proportion of gilts treated to induce puberty per generation for the selection line (S) and the control line (C).

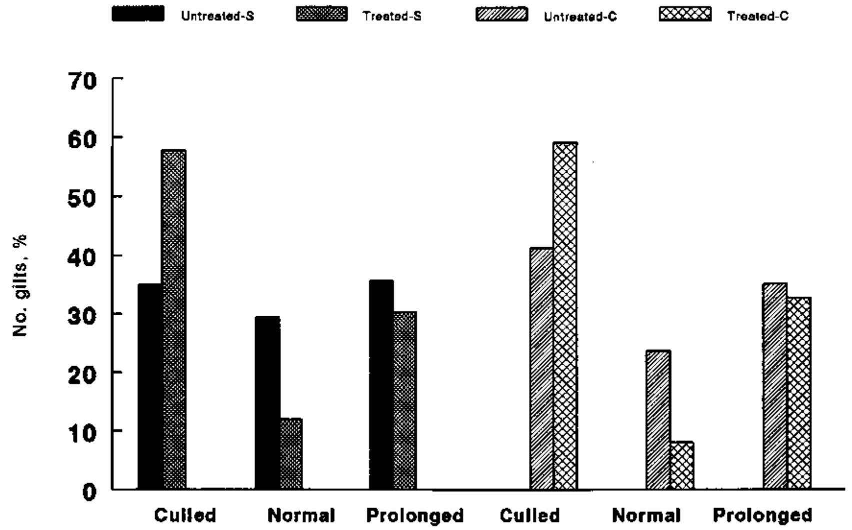

Figure 5. Proportion of gilts culled, gilts with a normal interval, and gilts with a prolonged interval from weaning to estrus for gilts untreated and treated to induce puberty for the selection line (S) and the control line (C).

The first principal component (**PC 1**) has high coefficients for measurements of litter size, litter weight, and body condition (Table 1). This component contrasts sows with a large and heavy litter at birth and weaning, a high loss of body condition during lactation, and a poor body condition at weaning, with sows with a small litter at birth and weaning, that have a minor loss of body condition. PC 1 can be interpreted as a general measure of sow productivity.

The second principal component (**PC 2**) has high positive coefficients for average piglet weight at birth and weaning, daily gain in litter weight, and litter weight at weaning, and high negative weights to numbers of piglets born, born alive, and dead during lactation. It contrasts sows with a good milk production, but a small litter, with sows with a poor milk production and a large litter.

Sows with a high value for the third principal component (**PC 3**) have poor body condition at farrowing, an above-average body condition score at weaning, and a minor loss of body condition during lactation. Their litters have above-average daily gain and weight at weaning. This PC contrasts sows with a poor body condition score at farrowing, a good performing litter, and without substantial loss of body condition, with sows in good condition at farrowing that suffer from a large loss of body condition and have a litter that gains below average.

The fourth principal component (**PC 4**) can be interpreted as a measure of poor mothering ability. Sows with a high value for PC 4 are characterized by a relatively high body condition at farrowing and weaning, high piglet and litter weights at birth, but a high number of dead piglets during lactation, and a small number of relatively heavy piglets weaned.

Sows with a prolonged interval from weaning to estrus differ most from sows with a normal interval for PC 1 (Table 2). Productive sows have a higher liability for a prolonged interval than other sows. Sows with a prolonged interval are also different with respect to PC 2 and PC 4. Good milk production (high daily gain in litter weight) and good mothering ability (very few piglets dead during lactation, high number weaned) increases the liability for a prolonged interval.

The largest difference between sows that were treated as a gilt to induce puberty and untreated sows was found in PC 2. Treated sows differ also with respect to PC 1 and PC 4. It means that treated sows are more likely than untreated sows to have a large litter that

Table 1. Eigenvectors used to calculate major principal components (PC 1 - PC 4).

Trait	PC 1	PC 2	PC 3	PC 4
Body condition farrowing pen	.039	.016	-.505	.511
Total number of pigs born	.350	-.382	.075	.119
Number of pigs born alive	.360	-.356	.088	.108
Weight of piglets at birth	.010	.370	.043	.323
Weight of litter at birth	.375	-.189	.101	.284
Number of pigs dead during lactation	-.079	-.397	-.066	.315
Number of pigs weaned	.419	.050	.096	-.245
Weight of piglets at weaning	-.071	.366	.160	.467
Weight of litter at weaning	.373	.311	.211	.089
Daily gain in litter weight	.353	.337	.218	.025
Age sow at weaning first litter	.094	-.101	.120	.075
Body condition at weaning	-.266	-.141	.357	.370
Loss of body condition	.273	.142	-.668	-.002

performs either poorly or well, but not intermediate, to have relatively poor body condition at farrowing and weaning, and few piglets that died during lactation.

Genetic parameters. Estimated heritabilities for breeding traits were low to moderate, and were highest for the body condition traits (Table 3). High genetic correlations were found between body condition loss and daily gain in litter weight, between pigs born alive and pigs dead during lactation, and between body condition loss and pigs born and born alive. Other high genetic correlations (number born with number born alive; body condition at weaning with body condition loss; body condition at farrowing with body condition at weaning) were high because of auto correlation.

Heritabilities of the major principal components were moderate (Table 4). Heritabilities of normal intervals, prolonged intervals, and incidence of prolonged intervals are all lower than the heritability of the interval from weaning to estrus of .36 reported in Ten Napel et al. (1995b). The genetic correlation between normal intervals and prolonged intervals was

Table 2. Percentage of variation explained, difference between sows with a normal and sows with a prolonged interval, and difference between untreated gilts and gilts treated to induce puberty, in standard deviation units.

	% variation	Prolonged - normal	Treated - untreated
PC 1	32.4	.310[b]	.178[a]
PC 2	21.0	.129[a]	-.532[b]
PC 3	10.4	-.043	-.014
PC 4	10.2	-.142[a]	-.182[b]

[a]Different from zero ($P < .05$)
[b]Different from zero ($P < .001$)

estimated at -.04. Because normal interval and prolonged interval can not both be observed on a sow, the residual correlation was held constant at zero. Heritability of treatment to induce puberty was moderate. Genetic correlations between breeding traits and interval from weaning to estrus were moderate to low (Table 5). Number of piglets that died during lactation had a positive genetic correlation, and body condition at farrowing and loss of body condition had negative genetic correlations with interval from weaning to estrus. The sign of the latter genetic correlation indicates that a genetic reduction of loss of body condition is accompanied by an increased interval from weaning to estrus, which is opposite to what one would expect. Genetic correlations with normal intervals had a sign different from those with prolonged intervals for body condition score at farrowing, daily gain in litter weight, loss of body condition, body condition score at weaning, and each of the four principal components. Phenotypic correlations were generally much lower than genetic correlations.

Genetic and environmental trends. None of the breeding traits showed a significant genetic trend within any of the lines (Table 6). Environmental trends were significant for body condition at farrowing, loss of body condition, number of piglets born alive, and daily gain in litter weight.

Table 3. Heritabilities (diagonal), genetic correlations (above the diagonal), and phenotypic correlations (below the diagonal) of breeding traits and interval from weaning to estrus.

	BCFARP	NBORNT	NBORNA	NDEADL	DGLITT	BCLOSS	BCWEAN
BCFARP	**.31**	.17	.29	.07	.18	.07	.64
NBORNT	.07	**.11**	.97	.30	.42	.39	-.15
NBORNA	.09	.92	**.26**	.44	.46	.37	-.06
NDEADL	.01	.29	.26	**.09**	.03	-.01	.01
DGLITT	.05	.21	.27	-.45	**.21**	.58	-.25
BCLOSS	.36	.24	.25	-.16	.41	**.18**	-.73
BCWEAN	.35	-.18	-.18	.17	-.37	-.75	**.33**

Abbreviations: BCFARP = body condition score at entering farrowing pen; NBORNT = total number of piglets born; NBORNA = number of piglets born alive; NDEADL = number of piglets which died during lactation; DGLITT = daily gain in litter weight during lactation; BCWEAN = body condition score at weaning; BCLOSS = loss of body condition during lactation; INTWE = interval from weaning to estrus

Table 4. Heritabilities (h^2) of principal components (PC 1 - PC 4) and interval traits.

Trait	h^2
PC 1	.21
PC 2	.11
PC 3	.13
PC 4	.30
Normal intervals, d	.18
Prolonged intervals, d	.17
Incidence of prolonged intervals	.27
Treatment to induce puberty	.28

Genetic contrasts. Average estimated breeding value of sows with a prolonged interval from weaning to estrus differed from that of sows with a normal interval for number of piglets

Table 5. Genetic, residual, and phenotypic correlations between breeding traits and interval from weaning to estrus, normal intervals and prolonged intervals.

	Interval weaning-estrus			Normal intervals			Prolonged intervals		
Trait	r_g	r_e	r_p	r_g	r_e	r_p	r_g	r_e	r_p
Body condition at entering farrowing pen, 0-5	-.20	-.02	-.08	.47	-.09	.05	-.26	.01	-.06
Total no. of pigs born	.10	.08	.08	.29	.02	.06	.10	.06	.06
No. pigs born alive	.14	.09	.09	.27	.04	.07	.15	.06	.07
No. pigs dead during lactation	.31	-.09	-.01	.34	-.15	-.09	.44	-.03	.03
Daily gain in litter weight, g/d	-.03	.15	.10	.34	.06	.11	-.19	.06	.01
Loss of body condition during lactation	-.24	.20	.08	.49	.19	.09	-.32	.08	.01
Body condition score at weaning, 0-5	.04	-.23	-.14	-.09	-.06	-.06	.08	-.09	-.05
PC 1	.05	.17	.13	.34	.06	.11	-.04	.09	.06
PC 2	-.24	.06	-.01	.09	.04	.05	-.39	-.02	-.07
PC 3	.37	-.07	.03	-.39	.04	-.03	.36	-.03	.03
PC 4	.00	-.11	-.07	.43	-.16	-.03	-.10	-.04	-.05

born, number of piglets born alive, daily gain in litter weight, loss of body condition, and body condition at weaning in the selection line (Table 7). In the control line the two groups of sows had different average estimated breeding values for body condition at farrowing, daily gain in litter weight, and body condition at weaning. Figure 6 shows the contrast in estimated breeding values per generation for each line for daily gain in litter weight, and loss of body condition. The contrast in estimated breeding values between sows with a normal interval and sows with a prolonged interval was not constant throughout the experiment, but varied across lines and generations.

Table 6. Genetic and environmental trend per generation for breeding traits within lines.

	Genetic		Environm.
Trait	Selection	Control	
Body condition score at entering farrowing pen, 0-5	.008	-.000	-.022[a]
Total no. piglets born	.006	-.000	.037
No. piglets born alive	.013	.002	.051[a]
No. piglets dead during lactation	-.010	.005	-.029
Daily gain in litter weight, g/d	3.50	.71	13.25[a]
Loss of body condition during lactation	.005	-.000	-.044[b]
Body condition score at weaning, 0-5	.000	-.000	.024

[a] Different from zero (P < .10)

[b] Different from zero (P < .001)

Discussion

Genetic selection for a short interval from weaning to estrus did not cause a measurable phenotypic or genetic trend in any of the breeding traits measured.

Principal component analysis is helpful for the interpretation of relationships between groups of traits, in this case breeding traits and rebreeding traits. It combines a large number of correlated traits into a smaller number of phenotypically uncorrelated linear combinations of the traits measured. These linear combinations are not necessarily genetically uncorrelated. The results of this analysis confirmed that the sow's performance during lactation, and even earlier, affects the liability for a prolonged interval (reviewed by Ten Napel et al., 1995a). Productive sows (PC 1) were more likely to have a delayed estrus after weaning, both phenotypically (Table 2) and genetically (Table 7). The relationship between rebreeding performance and PC 2 and PC 4 was mainly environmental.

Table 7. Differences in estimated breeding values for breeding traits between sows with a normal interval and sows with a prolonged interval within lines.

	Selection	Control
Body condition score at entering farrowing pen, 0-5	-.022	-.031[b]
Total no. of piglets born	.108[b]	.039
No. piglets born alive	.066[b]	.024
No. piglets dead during lactation	.001	-.011
Daily gain in litter weight, g/d	26.7[c]	14.0[b]
Loss of body condition during lactation	.035[b]	.012
Body condition score at weaning, 0-5	-.071[c]	-.055[c]
PC 1	.190[c]	.082[a]
PC 2	.008	.017
PC 3	.011	.011
PC 4	.014	-.057[a]

[a] Different from zero (P < .10)
[b] Different from zero (P < .05)
[c] Different from zero (P < .01)

Gilts treated with hormones to induce puberty had a higher probability of being removed from the experiment than untreated gilts (Figure 5). This, however, may be a coincidental rather than a causal relationship. Gilts were treated after 3 wk of the 4 wk mating period. Two weeks after the end of the mating period, all gilts were girth-tethered for the first time. Technicians confirmed that this was a considerably stressful condition for the gilts. So treated gilts were girth-tethered in the second or third week of gestation, which is the period in which embryo's attach to the uterine wall. Stress in this period causes considerable embryonic loss and return to estrus (Van der Lende, 1994). Gilts that returned to estrus after mating were removed from the experiment in order to maintain the mating design.

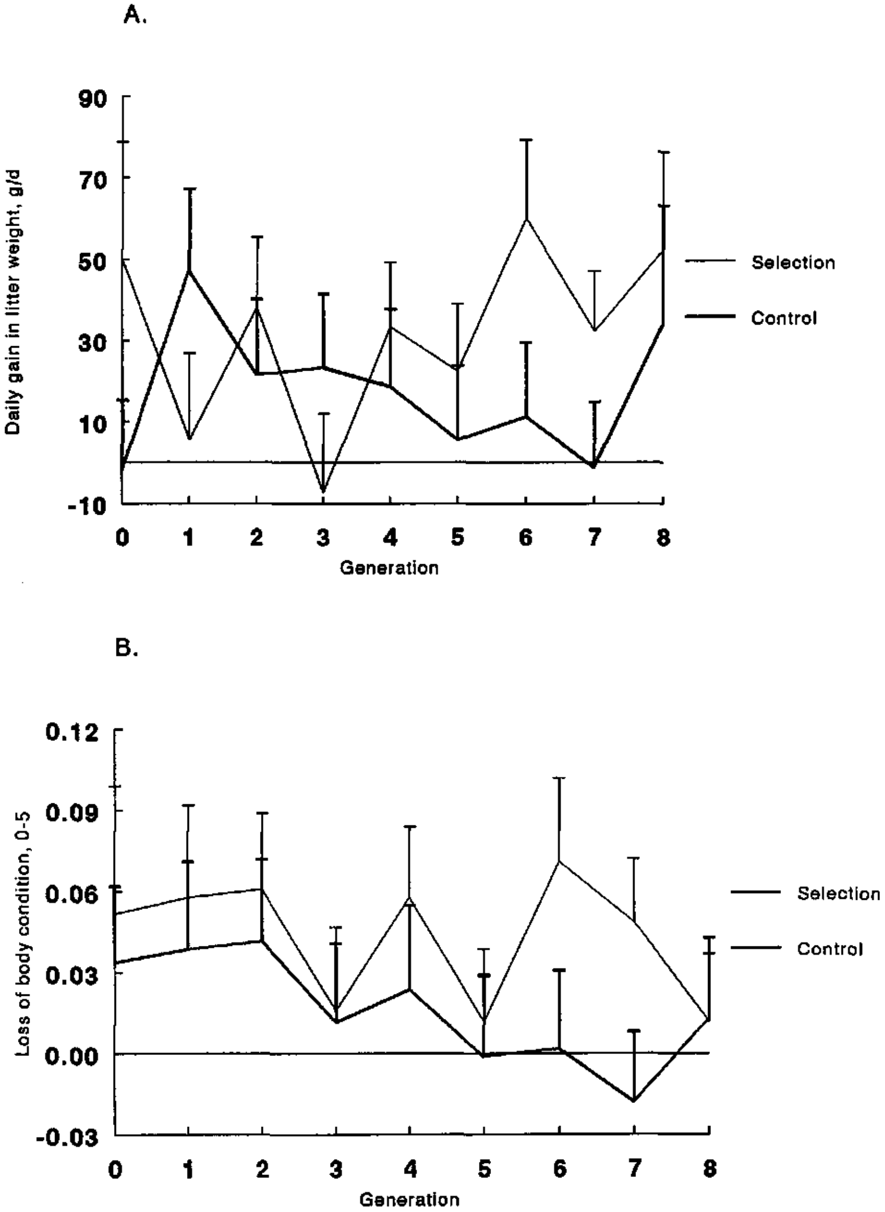

Figure 6. Development of differences in estimated breeding value between sows with a normal interval and sows with a prolonged interval within lines across generations for average daily gain in litter weight (A) and loss of body condition (B).

The probability of being treated with hormones to induce puberty showed substantial genetic variation. It is likely that the procedure of not selecting treated sows as a dam in the selection line caused the decrease in incidence of treatment observed in the selection line.

Among the gilts with an observed interval from weaning to estrus, gilts treated to induce estrus had a lower probability of having normal resumption of cyclic activity than untreated gilts. Whether this phenotypic association has a genetic basis is difficult to establish, but if this is the case, then the practice of not selecting treated gilts as a dam caused a response in the same direction as selection for a short interval from weaning to estrus.

When genetic relationships between two traits are studied in a set of data from a population selected for a third trait, then the third trait should be included in the analyses, in order to get unbiased estimates (Pollak et al., 1984). In this particular case we did not know how to include the trait under selection in the analysis properly, so we decided not to include a third trait in the analysis, when estimating genetic parameters (Table 3, 4 and 5).

In a review (Ten Napel et al., 1995a), we concluded that several conditions, such as a severely catabolic state, a severe loss of body tissue, and peri- or postweaning stress, may cause a delayed estrus after weaning. It is likely that in a given population and environment, more than one of these conditions contribute to the occurrence of prolonged intervals. This situation causes underestimation of genetic contrasts between sows with a normal and sows with a prolonged interval, genetic trend as a correlated response of selection for a short interval from weaning to estrus, and genetic correlations with incidence of a prolonged interval. This can be explained as follows. Assume three traits ($i=1,3$) cause prolonged intervals independently. For each trait there is a threshold; if one (or more) of the traits supersedes its threshold, then the interval from weaning to estrus becomes prolonged, otherwise it is normal. In Figure 7, the distribution of one of the three traits is shown. T denotes the threshold, and sows with a prolonged interval because of trait i are in the shaded area of the graph. Let p_i be the fraction of sows with a prolonged interval, that have a value for trait i that supersedes the threshold for that trait. (Note that if for some sows more than one trait supersedes its threshold at the same time, then the sum of the p_i's is larger than 1.) Further, let C_i be the difference in estimated breeding values for trait i between sows with a normal interval (μ_n) and sows with a prolonged interval, *caused by trait i* (μ_p). Sows with a prolonged interval because of a condition other than trait i have average estimated breeding value μ_n, when the traits are uncorrelated. C_i increases in size, when the distance between the over-all mean μ_i and the threshold T_i increases, but does not change much when p_i is between .1 and .9.

Usually the exact cause of a prolonged interval is unknown, so the observed contrast in estimated breeding value for trait i is

$$\hat{C}_i = [p_i.\mu_p + (1-p_i).\mu_n] - \mu_n = p_i.C_i \tag{7}$$

Observed contrasts, therefore, may vary across generations and lines to a large extent when p_i varies. The relative contribution p_i may change due to the selection applied, genetic drift, changes in management or environment, or random changes. This explains that for some traits a significant contrast was observed in the one line, but not in the other. It also explains the variation in observed contrasts across generations shown in Figure 6.

Suppose we select on trait i, and after t generations, the cumulated response in trait i is μ_t-μ_0=$\Delta\mu$. The correlated response in incidence of prolonged intervals is then

$$\Delta n_1 = \left[\int_{T_i}^{\infty}\varphi\left(\frac{x-\mu_{i,t}}{\sigma}\right).dx - \int_{T_i}^{\infty}\varphi\left(\frac{x-\mu_{i,0}}{\sigma}\right).dx\right] \tag{8}$$

If we want to achieve $\Delta\mu$ as a correlated response of selection against prolonged intervals, the direct response of selection needs to be

$$\Delta n_2 = \left[\int_{T_i}^{\infty}\varphi\left(\frac{x-\mu_{i,t}}{\sigma}\right).dx - \int_{T_i}^{\infty}\varphi\left(\frac{x-\mu_{i,0}}{\sigma}\right).dx\right] \cdot \frac{\Sigma h_j^2 \cdot p_j}{h_i^2 \cdot p_i} \tag{9}$$

which is higher than Δn_1, unless no other trait causing prolonged intervals shows genetic variation. It means that Δn_2 needs to be substantial, in order to be able to detect $\Delta\mu$ different from zero. When the change in incidence of prolonged intervals is rather slow, like in the

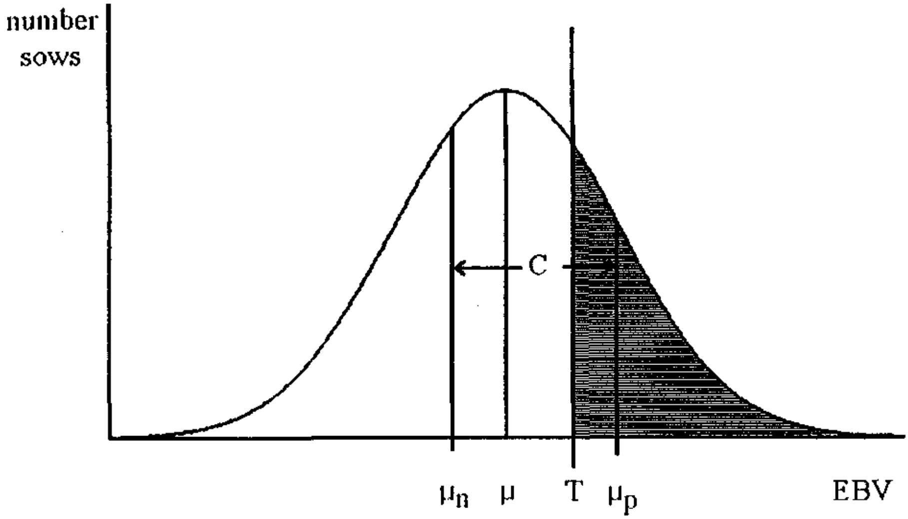

Figure 7. Difference (C) between average estimated breeding value of sows with a normal interval for trait i (μ_n) and average estimated breeding value of sows with a prolonged interval (μ_p)

selection experiment reported herein, the genetic trend in trait i is likely to become undetectable.

The consequence of the above is that a significant observed contrast for trait i in this selection experiment is evidence that this trait affects incidence of prolonged intervals, but if no significant contrast was found, then a correlated response in incidence of prolonged intervals due to selection on trait i may still be substantial.

Selection against prolonged intervals causes a correlated response in each of the traits causing prolonged intervals. The absolute incidence of prolonged intervals due to each of the traits decreases, but the relative contribution of the traits to incidence of prolonged intervals remains fairly constant, unless the heritabilities of the traits are very different. Selection for trait i causes an absolute increase in incidence of prolonged intervals due to trait i, but incidence of prolonged intervals due to other traits remains unchanged. Thus, the relative contribution (p_i) of the trait under selection increases, whilst the relative contributions of other traits decrease. Therefore, it is more efficient to study genetic relationships between rebreeding performance and trait i in populations selected for trait i, than in unselected populations or populations selected for another trait, because the observed contrast for trait i is likely to be higher in populations selected for trait i, than in other populations.

The differences in average estimated breeding values between sows with a normal interval and sows with a prolonged interval (Table 7) are evidence that selection for sow productivity may increase the genetic liability for a prolonged interval. In fact, this was observed in a selection experiment on 21-d litter weight and litter size, in which an increased interval from weaning to estrus was observed (Shurson and Irvin, 1992).

One might expect that if a trait causes prolonged intervals above a certain threshold, then a more severe state of this trait causes a more severely prolonged interval. This does not seem to hold for the traits associated with metabolic loss, except for body condition score at farrowing. Daily gain in litter weight (as a measure of milk production) and loss of body condition have a negative genetic correlation with the length of the prolonged interval. Sows with a severe loss of body tissue should be able to recover in up to 6 or 7 weeks, when provided with an adequate diet, and resume cyclic activity soon after recovery. Prolonged intervals that are much longer are likely to have a different cause (e.g. cystic ovaries, because this condition may cause severely prolonged intervals, and it is presumably unrelated to metabolic imbalance). Sows with severely prolonged intervals were intermediate for daily gain in litter weight or loss of body condition, which probably caused a correlation with different sign.

Splitting a sorted set of observations on a trait into two groups, and analysing the selected groups separately, yields estimates for heritabilities and correlations that deviate from the estimates from the original set. Such an analysis is difficult to interpret in general, because a selected set of observations is omitted from the analysis. For normal and prolonged intervals, however, the situation is different, because we consider them as separate traits measured on the same scale. The difference between traits is whether problems delay onset of cyclic activity. The distinction is supported by the estimate of the genetic correlation between normal and prolonged intervals, which is essentially zero.

Genetic analysis of the interval from weaning to estrus may not be proper, if it is not taken into account whether the interval was normal or prolonged, because normal and prolonged intervals are regressed to a common mean, that is dependent on the incidence of prolonged intervals. This makes it difficult to compare the estimate of the heritability of the interval from weaning to estrus with those of the three components. Also genetic correlations with interval from weaning to estrus, interval from weaning to farrowing, or farrowing interval may not be useful for predicting a correlated response in these traits.

In conclusion, selection for a short interval from weaning to estrus did not cause a measurable phenotypic or genetic trend in any of the breeding traits measured in the selection experiment reported in this paper. We have argued, however, that the reverse does not hold, i.e. genetic selection for some of these traits may change the genetic liability for a prolonged interval as a correlated response.

Implications

Correlated responses to selection for a short interval from weaning to estrus are difficult to measure, and depend highly on the environment in which the population is selected. Selection for breeding traits, however, may cause a correlated response in incidence of prolonged intervals, even if no correlated response selection for a short interval from weaning to estrus on the trait was observed. Genetic relationships between any trait and rebreeding performance should be studied taking into account that intervals from weaning to estrus consist of normal intervals and prolonged intervals.

Acknowledgement

The authors would like to thank B. Kemp and T. van der Lende for discussion and careful reading of the manuscript.

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Chapter 6

Genetics of Interval from Weaning to Estrus in First-Litter Sows. III. Correlated Responses on Rearing Traits

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Submitted for publication in Journal of Animal Science.

Abstract

Data on rearing performance of 3777 Dutch Landrace gilts from a selection experiment on a short interval from weaning to estrus were available to study correlated responses to selection, and to estimate relationships between rearing traits and rebreeding performance. Correlated responses to selection were studied by estimating phenotypic and genetic trends. Relationships with rebreeding performance were studied by estimating phenotypic, genetic and residual correlations with length of normal interval from weaning to estrus and length of prolonged interval from weaning to estrus, and the difference in phenotype and average EBV between sows with a normal interval and sows with a prolonged interval. Principal components were derived from the entire set of rearing traits, and those accounting for more than 10% of the variation were analyzed as new traits. Neither average daily gain in the nursing pen (weaning to 25 kg; DGNURS), average daily gain in the rearing pen (25 to 90 kg; DGREAR), body condition score at entering mating pen (BCMATP), nor any of the principal components showed a phenotypic or genetic trend due to selection. DGREAR and BCMATP and two of the four principal components had genetic correlations with the length of normal intervals of different sign than those with the length of prolonged intervals. A small difference in average EBV was found for BCMATP in the selection line. The EBV for the first principal component, interpreted as a measure of consistent good growth ability, differed between sows with normal and sows with prolonged intervals in the control line. It was concluded that the decrease in incidence of prolonged intervals in the selection line was not achieved by a change in rearing performance.

Key words: Rebreeding, Selection, Correlated Responses, Growth

Introduction

A delayed return to estrus after weaning is mainly a problem in first-litter sows (Hurtgen and Leman, 1981; Maurer, 1985). Intervals from weaning to estrus, mating or farrowing can be categorized into normal intervals and prolonged intervals (Ten Napel et al., 1995a; Ten Napel and Johnson, 1995).

Management procedures and housing conditions affect the liability for having a prolonged interval from weaning to estrus to a large extent. In a relatively standardized environment it was observed that genetic selection for a short interval from weaning to estrus reduced the average interval by decreasing the incidence of prolonged intervals, rather than affecting the mean interval from weaning to estrus of sows with a normal interval or the mean of those with a prolonged interval (Ten Napel et al. 1995a). Ten Napel et al. (1995b) showed that this reduction was not accompanied by a trend in the breeding traits measured, but they found differences in average estimated breeding values for some of these traits between sows with normal and prolonged intervals, indicating that selection for these breeding traits might increase the number of sows with a prolonged interval.

Ten Napel and Johnson (1995) concluded from analyses of field data that genetic selection for increased daily gain and reduced backfat might increase the liability for a prolonged interval. Genetic selection for a short interval from weaning to estrus, therefore, may have caused a change in growth performance of gilts in unfavorable direction.

The aim of this study was to evaluate relationships between rearing performance as a gilt and rebreeding performance after weaning the first litter, and to estimate trends in rearing traits due to selection for a short interval from weaning to estrus. Phenotypic contrasts between sows with a normal interval and sows with a prolonged interval were estimated to compare causes of prolonged intervals in this experiment with those in other studies. Genetic contrasts were estimated instead of genetic correlations with incidence of prolonged intervals, because invalid assumptions were required in the latter analysis.

Materials and Methods

General. Data were available from Dutch Landrace sows from a selection experiment on a short interval from weaning to estrus after weaning the first litter. Selection was applied only in the selection line, and not in the control line. The experimental population comprised a foundation population (generation 0), seven generations of intensive selection, and one generation of relaxed selection (generation 8). Selection and management procedures were described in Ten Napel et al. (1995a).

Traits recorded from birth to entering the mating pen were weight at birth (within 24 h after birth), weaning age and weight, age and weight at moving from the nursing pen (flatdecks) to the rearing pen, age and weight at moving from the rearing pen, and age and body condition score at moving to the mating pen. Body condition was evaluated by experienced technicians, on a well-defined eleven-class scale, ranging from 0 to 5 with steps of ½. A body condition score of 0 means that the gilt was very thin, and 5 means a thick fat cover. Hormonal induction of puberty was applied after the third week of the 4-wk mating period to obtain a sufficient number of gilts mated in the mating period (Ten Napel et al., 1995a,b).

Phenotypic trends. Phenotypic least-squares means of the traits measured were estimated with the REML procedure in Genstat (Genstat 5 Committee, 1993), using a model including line-generation and mating group within line-generation as fixed effects. For daily gain in the nursing pen, age at weaning and age at moving to the rearing pen were included as covariables, and age at moving to the rearing pen and age at moving from the rearing pen were added as covariables for daily gain in the rearing pen, in addition to the above model.

Phenotypic contrasts. The principal component analysis was done using PROC PRINCOMP in the SAS statistical package (SAS, 1985). For details about the background, the use and interpretation of this method, see Brown et al. (1973), Young et al. (1977) and Ten Napel et al. (1995b). A total of 904 selection-line gilts and 843 control-line gilts had complete records, and were included in this analysis.

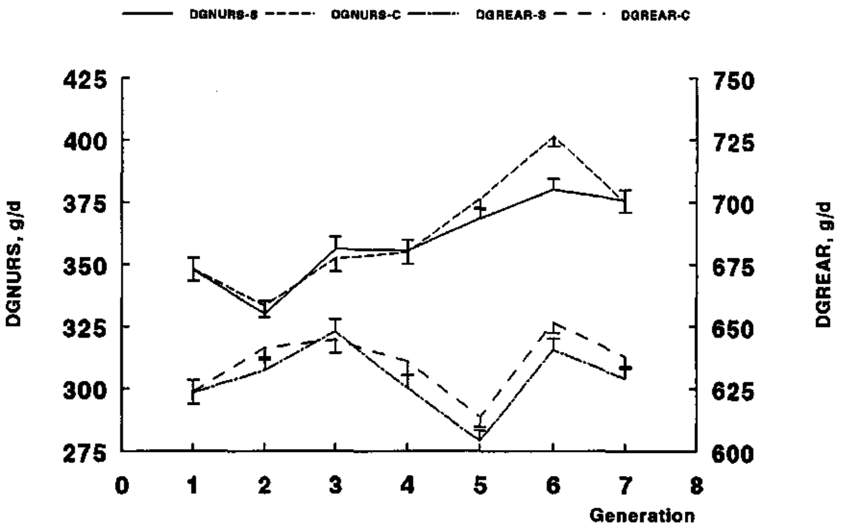

Figure 1. Average daily gain in the nursing pen (DGNURS) and in the rearing pen (DGREAR) per generation within the selection line (S) and the control line (C).

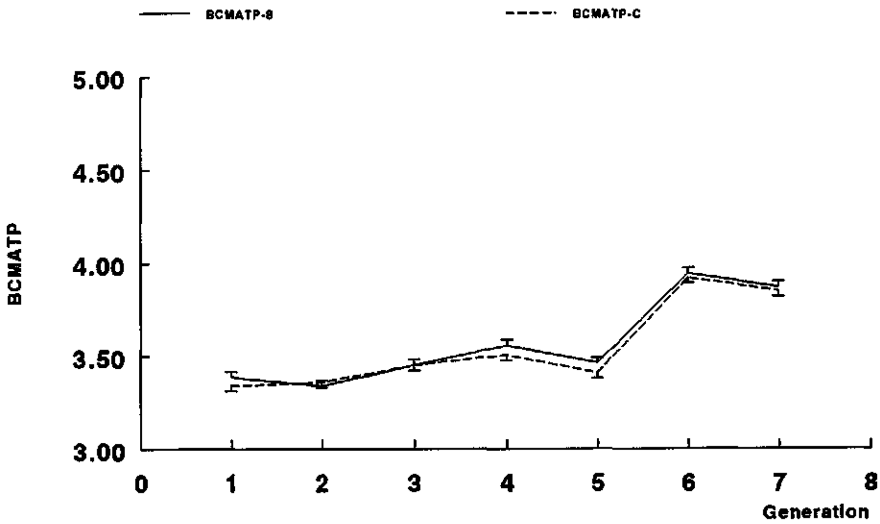

Figure 2. Body condition score at entering the mating pen (BCMATP) per generation within the selection line (S) and the control line (C).

Genetic parameters. The general model for estimating components of variance and covariance was as follows: $\mathbf{Y} = \mathbf{Xb} + \mathbf{Wc} + \mathbf{Zu} + \mathbf{e}$, where $\mathbf{Y}$ is a vector of observations, $\mathbf{X}$, $\mathbf{W}$, and $\mathbf{Z}$ are known design matrices for fixed effects ($\mathbf{b}$), common environmental effects ($\mathbf{c}$), and genetic effects ($\mathbf{u}$), and $\mathbf{e}$ is a vector of residuals. Fixed effects were the covariables described above, and the combination of generation and mating group. The sow that suckled the gilt as a piglet was included in the model as a common environmental effect, with $\mathrm{var}(\mathbf{c})=\mathbf{I}\sigma$. Gilt was included as an animal genetic effect, with $\mathrm{var}(\mathbf{u})=\mathbf{A}\sigma$. The covariance structure of residuals was $\mathrm{var}(\mathbf{e})=\mathbf{I}\sigma$. Covariances between $\mathbf{c}$, $\mathbf{u}$, and $\mathbf{e}$ were assumed zero.

A derivative-free REML algorithm, as applied in the MTDFREML programs (Boldman et al., 1993), was used to estimate components of variance. Estimated breeding values were obtained from these analyses after the convergence criterion for variance component estimation was met. Data from 1881 selection-line gilts and 1896 control-line gilts were included in these analyses.

Genetic contrasts, genetic trends, and environmental trends were estimated as described in Ten Napel et al. (1995b).

Results

Phenotypic trends. Figure 1 and 2 show development of least-squares means within lines over generations for daily gain in the nursing pen, daily gain in the rearing pen and body condition score at entering the mating pen. Only daily gain in the nursing pen in generation 6 was different between lines ($P < .05$). Within-line means for these traits did not diverge during the experiment.

Phenotypic contrasts. The major principal components obtained for the traits measured between birth and mating are presented in Table 1. The coefficients of the first principal component (PC 1) are similar in magnitude. The weight and gain traits have a positive sign, and the age traits have a negative sign. This principal component can be interpreted as a measure of consistent good growth ability. This component creates a contrast between gilts that gained very well and were heavy at young age, and gilts that did not gain very well, and had a below-average weight at a fairly old age.

Table 1. Eigenvectors used to calculate major principal components (PC 1 - PC 4)

Trait	PC 1	PC 2	PC 3	PC 4
Birth weight	.272	-.167	-.152	.486
Weight at weaning	.396	-.247	.035	.321
Average daily gain in nursing pen	.387	-.050	.491	.062
Age at start of rearing period	-.254	.536	.220	-.099
Weight at start of rearing period	.294	.327	.610	.001
Average daily gain in rearing pen	.388	.202	-.375	-.372
Age at end of rearing period	-.318	.422	-.096	.424
Weight at end of rearing period	.324	.422	-.362	.090
Age at moving to mating pen	.058	.218	.046	.551
Body condition score at moving to mating pen	.328	.305	-.175	-.130

The second principal component (PC 2) has high coefficients for age traits, and weight and gain traits after moving to the rearing pen, and a negative coefficient for weaning weight. Gilts with a large value for this component had above-average weight and gain records, because they were weighed at a relatively old age.

A large value for the third principal component (PC 3) indicates that the gilt initially performed well, but did not do very well after moving to the rearing pen. The fourth component (PC 4) contrasts gilts that were relatively heavy at birth and weaning, relatively old at moving from the rearing pen and at moving to the mating pen, and with a poor daily gain in the rearing pen, with gilts that weighed below average at birth and weaning, but grew very well in the rearing pen.

Table 2 shows that gilts that had a prolonged interval after weaning the first litter and gilts with a normal interval had on average different values for PC 1 and PC 3. Gilts with a normal interval had a better over-all growth ability, than gilts with a prolonged interval. Poor performance in the rearing pen after initially good growth in the nursing pen increased the probability of a prolonged interval. Differences between gilts treated to induce puberty and untreated gilts were significant for PC 1, PC 3, and PC 4. Gilts with a below-average growth,

Table 2. Percentage of variation explained, difference between sows with a normal and sows with a prolonged interval, and difference between untreated gilts and gilts treated to induce puberty, in standard deviation units.

	% variation	Prolonged - normal	Treated - untreated
PC 1	28.1	-.128[a]	-.262[b]
PC 2	17.1	-.038	-.096
PC 3	14.0	.095[a]	.160[a]
PC 4	11.1	.073	-.202[b]

[a]Different from zero ($P < .05$)

[b]Different from zero ($P < .001$)

in general or after good growth in the nursing pen, were more likely to be treated to induce puberty. Also gilts that were young at entering the mating pen, with a low birth and weaning weight, but a good growth in the rearing pen, had a higher probability of being treated.

Genetic parameters. Heritabilities, and genetic and phenotypic correlations are presented in Table 3. Genetic correlations among the rearing traits were moderate to high. Proportion of variance due to common environment, common environmental and residual correlations are shown in Table 4. Proportion of variance due to common environment was lower when the time between weaning and measuring the trait was longer. Heritabilities of the principal components were moderate to low (Table 5). Genetic correlations of normal intervals and prolonged intervals with daily gain in the rearing pen, body condition score in the mating pen, PC 1 and PC 3 had different sign (Table 6).

Genetic and environmental trends. No significant genetic trend was observed for any of the traits (Table 7) or principal components. Environmental trends were observed in daily gain in the rearing pen, and in body condition score at moving to the mating pen.

Genetic contrasts. A difference in average estimated breeding values between sows with a normal and sows with a prolonged interval from weaning to estrus was found in the selection line for body condition score at entering the mating pen, albeit small compared to the unit of scoring, and in the control line for PC 1 (Table 8).

Table 3. Heritabilities (diagonal), genetic correlations (above the diagonal), and phenotypic correlations (below the diagonal) among rearing traits.

	DGNURS	DGREAR	BCMATP
Average daily gain in nursing pen (DGNURS)	**.18**	.32	.52
Average daily gain in rearing pen (DGREAR)	.03	**.24**	.55
Body condition score in mating pen (BCMATP)	.18	.45	**.37**

Table 4. Proportion of variance due to common environment (diagonal), common environmental correlations (above the diagonal), and residual correlations (below the diagonal) among rearing traits.

Trait	DGNURS	DGREAR	BCMATP
Average daily gain in nursing pen (DGNURS)	**.25**	-.04	-.17
Average daily gain in rearing pen (DGREAR)	-.04	**.11**	.43
Body condition score in mating pen (BCMATP)	.11	.40	**.04**

Discussion

None of the traits studied showed a detectable trend as a correlated response of selection for a short interval from weaning to estrus.

The principal component analysis showed a phenotypic relationship between rearing performance and rebreeding performance (Table 2), but this relationship is mainly environmental. It was only for PC 1, that a difference in average estimated breeding values between sows with normal prolonged intervals was found. Comparing the results with those in the accompanying paper (Ten Napel et al., 1995b), shows that in the selection experiment

Table 5. Heritabilities (h^2) and proportion of variance due to common environmental effects (c^2) of principal components and interval traits

Trait	h^2	c^2
PC 1	.31	.22
PC 2	.12	.36
PC 3	.02	.30
PC 4	.25	.41

Table 6. Genetic, residual, and phenotypic correlations between rearing traits and normal and prolonged interval from weaning to estrus.

	Normal intervals			Prolonged intervals		
Trait	r_g	r_e	r_p	r_g	r_e	r_p
Average daily gain in nursing pen	.20	.01	.05	.25	.00	.05
Average daily gain in rearing pen	.08	-.07	-.03	-.27	-.07	-.11
Body condition score in mating pen	.15	.00	.04	-.22	-.04	-.08
PC 1	.18	-.02	.03	-.27	-.01	-.07
PC 2	.02	-.04	-.02	-.01	-.01	-.01
PC 3	-.07	.04	.02	.62	.08	.10
PC 4	-.15	.08	.01	-.52	.22	.01

breeding traits were more important contributors to genetic variation in rebreeding performance than rearing traits.

PC 3 had a high positive genetic correlation with the length of a prolonged interval. Although information is lacking, it may be that the main reason for severely prolonged intervals (> 50 d) is the occurrence of cystic ovaries. A possible explanation is the following. Gilts with a high value for PC 3 performed well in the nursing pen, but after mixing into new groups, their growth rate was below average. Mixing is a considerable stressor, so among the gilts with a high value for PC 3 may be gilts with a high physiological response to stressors, such as chronically elevated levels of corticosteroids, which reduces weight gain (Broom and

Table 7. Genetic and environmental trend per generation for rearing traits within lines.

	Genetic		Environm.
Trait	Selection	Control	
Average daily gain in nursing pen, g/d	-.912[b]	.122	8.824[a]
Average daily gain in rearing pen, g/d	-.392	.649	1.847
Body condition score, 0 - 5	.006	.001	.054[a]

[a]Different from zero (P < .001)

[b]Different from zero (P < .10)

Table 8. Differences in estimated breeding values for rearing traits and principal components between sows with a normal interval and sows with a prolonged interval within lines.

	Selection	Control
Average daily gain in nursing pen, g/d	1.17	-.91
Average daily gain in rearing pen, g/d	-1.34	-1.35
Body condition at entering mating pen, 0-5	-.033[a]	-.018
PC 1	-.023	-.103[b]
PC 2	-.018	-.020
PC 3	.002	.003
PC 4	.025	.002

[a]Different from zero (P < .10)

[b]Different from zero (P < .05)

Johnson, 1993). If these gilts respond to the stressor of weekly moving to a new pen after weaning in the same way, they may be more liable to develop cystic ovaries (Ryan and Raeside, 1991a,b), than other sows. Hennessy et al. (1988) showed that differences in adrenal response to ACTH challenge among individual pigs were large and repeatable.

This study does not confirm the results of Ten Napel and Johnson (1995), who found that average estimated breeding values for test traits were different between sows with a normal interval from weaning to farrowing and sows with a prolonged interval from weaning to farrowing, but at the same time, the results are not contradictory. If a genetic relationship exists, it is more likely to estimate a significant genetic relationship between average daily gain or backfat depth and incidence of a prolonged interval in a population selected for daily gain and (or) backfat, than in a population selected for a short interval from weaning to estrus (Ten Napel et al., 1995b). Further, the two populations originated from different breeds, and were managed in a different way, which may have caused differences in incidence of causes of a prolonged interval.

In conclusion, genetic selection for a short interval from weaning to estrus did not cause a measurable change in any of the rearing traits studied. There was no evidence in this study that selection on average daily gain or body condition score will cause an increasing incidence of prolonged intervals from weaning to estrus as a correlated response.

Implications

The results of this study do not reveal a relationship between rearing performance and rebreeding performance, but the results do not imply that no relationship exists. Although no evidence was found in this study, it may well be that genetic selection for rearing (or fattening) traits increase incidence of prolonged intervals from weaning to estrus.

Acknowledgement

The authors would like to thank B. Kemp, R. K. Johnson and T. van der Lende for discussion and careful reading of the manuscript

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Chapter 7

Selection strategies for rebreeding performance and production

Jan ten Napel
Theo Meuwissen

Abstract

A simulation study was set up to compare three different methods of selection against prolonged intervals from weaning to estrus, namely I. culling after a given period of anestrus, II. EBV for interval from weaning to estrus, either with complete recording or with culling after 21 d of anestrus, and III. EBV for the occurrence of a prolonged interval, recorded as a binary trait. A 120-sow unit was simulated with selection going on for 9 generations. Primary trait was a growth trait, with a positive (unfavorable) genetic correlation (.1 or .35) with a trait causing prolonged intervals above a threshold. EBV's in strategy II and III were combined in an index. It was considered not appropriate to base weightings in the index solely on economic criteria, so a range of index weightings was used for each strategy. When the response in growth is equal to the reference situation (univariate analysis of EBV for growth without culling for anestrus), strategy III outperformed I and II. Strategy III gave the lowest decrease in incidence of normal interval when r_g*=.35, and the highest increase in incidence of normal intervals when* r_g*=.1. It was concluded that strategy III is the best method to select against prolonged intervals, but in practice differences between methods will probably be smaller than in this study.*

Key words: Rebreeding, Selection, Reproduction, Sow

Introduction

To prevent an increase in incidence of prolonged intervals from weaning to estrus as a correlated response to selection for economically important traits, one can improve management, and the problem will be reduced for some time. A more structural approach is to reduce the genetic liability for a prolonged interval. In this paper a simulation study is

Table 1. Means, phenotypic variances, heritabilities (in bold on the diagonal), genetic correlations (above the diagonal) and environmental correlations (below the diagonal) used for simulation of data.

Trait	μ	σ^2_p	GROWTH	UND	NORM	PROL
Growth (GROWTH)	550	4718	**.23**	.10 or .35	.08	-.27
Underlying trait (UND)	-.80	1.37	.02	**.27**	.00	.00
Normal interval, d (NORM)	5.5	.85	-.07	.00	**.18**	.00
Prolonged interval, d (PROL)	28.28	800	-.07	.00	.00	**.17**

described with the purpose to compare several strategies of genetic selection against prolonged intervals.

Material and methods

General. For reasons of clarity, it is assumed that there is only one economically important growth trait (referred to as 'growth'), which is subject to genetic selection, and is unfavorably correlated with a trait that causes prolonged intervals above a certain threshold. It is also assumed that there is only one trait causing prolonged intervals. Rebreeding performance is measured as the interval from weaning to estrus. Each estrus is expressed and observed (i.e. no silent estrus).

Population characteristics. A 120-sow nucleus unit was simulated, with selection going on for 9 generations. All sows are replaced after the first parity, although in practice interval from weaning to estrus would not be important in that case. The test capacity is 480 animals per generation, and if possible, two boars and two gilts from each litter are put on test. Each generation, a total of 10 boars and 120 gilts are selected after the end of the test. At the time of selection, gilts do not have an observed interval from weaning to estrus.

Data simulation. In order to simulate interval from weaning to estrus, three traits were generated, namely the underlying trait causing prolonged intervals above a certain threshold, a normal interval and a prolonged interval. If the underlying trait was lower than the fixed threshold, the normal interval was assigned to the interval from weaning to estrus, and otherwise to the prolonged interval. With the mean of the underlying trait at -0.80, the threshold at 0.0, and the variance being 1.37 (Table 1), the incidence of normal intervals in the base generation is 75%.

Parameters needed for simulation were set to the values estimated for average daily gain in the rearing pen (Ten Napel et al., 1996b), except for the genetic correlation with the trait underlying occurrence of a prolonged interval, which was set to .10 and .35. Heritabilities for the components of the interval from weaning to estrus were set to the values presented in Ten Napel et al. (1996a), and genetic and residual correlations between these components were set to zero. Parameters are shown in Table 1.

Additive genetic values of animals in the base population for each trait were simulated from a multivariate normal distribution. The additive genetic value of animal i for trait j in a subsequent generation was simulated as:

$$u_{ij} = \frac{1}{2}u_{sij} + \frac{1}{2}u_{dij} + \phi_{ij} \qquad [1]$$

where u_s and u_d are the additive genetic values of the sire and the dam, and ϕ_{ij} is the mendelian sampling term, sampled from a multivariate distribution. Variance of mendelian sampling terms was not reduced as caused by inbreeding.

Residuals for all animals for each trait were also simulated from a multivariate normal distribution. For growth, the underlying trait, and the normal interval, phenotypic values were generated as:

$$y_{ij} = \mu_j + u_{ij} + e_{ij} \qquad [2]$$

where μ_j is the mean of trait j, and e_{ij} is the residual for animal i and trait j. Simulating a phenotypic value for a prolonged interval is not straightforward, if both the correlation

Table 2. Parameters used to estimate breeding values.

	h^2_1	h^2_2	r_g	r_e	σ^2_{p1}	σ^2_{p2}
Strategy I	.23	-	-	-	4718	-
Strategy IIa	.23	.10	.13	-.01	4718	404.1
Strategy IIb	.23	.07	.48	.01	4718	10.23
Strategy III	.23	.27	.10 or .35	.02	4718	1.37

structure, and the characteristic of having an exponential distribution should be taken into account. The procedure used is described in detail in the Appendix.

Criteria of selection. The selection strategies compared were:

Reference: Selection is based on estimated breeding values for growth only, estimated in a univariate analysis. Rebreeding performance is not taken into account.

Strategy I: Selection is based on estimated breeding values for growth, estimated in a univariate analysis. In addition, sows anestrous after a given number of days are culled, and their progeny is not put on test. Open test places that arise are filled by increasing the number of progeny put on test of good sows to eight. If this was not sufficient, it was accepted that part of the test places was not used.

Strategy IIa: Selection is based on an index of estimated breeding values for growth and interval from weaning to estrus, obtained from a bivariate analysis. All intervals are recorded.

Strategy IIb: Selection is based on an index of estimated breeding values for growth and interval from weaning to estrus, obtained from a bivariate analysis. Sows are culled after 21 d anestrus, and these sows have missing values for interval from weaning to estrus.

Strategy III: Selection is based on an index of estimated breeding values for growth and occurrence of a prolonged interval, recorded as a binary trait. Breeding values were obtained from a bivariate analysis.

For strategy I, days at culling were 7, 14, 21, and 28 d. For strategy IIa, IIb and III, estimated breeding values of the traits were combined in the following index:

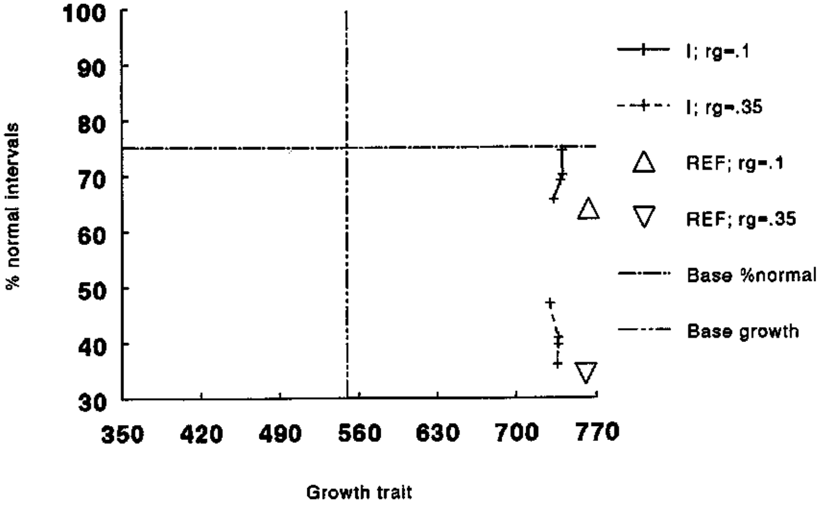

Figure 1. Response in growth and incidence of normal intervals, due to genetic selection for growth combined with independent culling for anestrus (Strategy I). The highest incidence of normal intervals refers in both cases to culling after 7 d.

$$I = EBV_{growth} - b * EBV_{rebreeding},$$

where the rebreeding trait is interval from weaning to estrus for strategy IIa and IIb, and occurrence of a prolonged interval for strategy III. We feel that the choice of weightings in the indices should not be based solely on economic criteria. In a sustainable pig production system, it is not acceptable that rebreeding performance dramatically impairs, when the benefits of improved production cancel out the additional costs of long intervals, increased culling and hormonal treatment. Instead, a number of alternatives were studied for each strategy, in order to establish a relationship between the response in growth and the response in rebreeding performance, as a function of the weighting in the index. The weightings in the index for the rebreeding trait (b) were varied from .1, .5, 1, 2, 5, 10, 20 to 30.

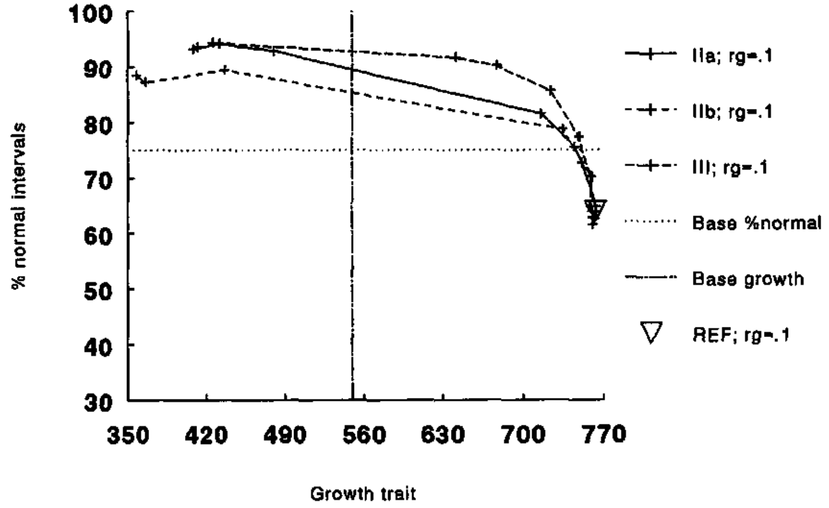

Figure 2. Response in growth and incidence of normal intervals due to genetic selection for growth and (IIa) interval from weaning to estrus with complete recording; (IIb) interval from weaning to estrus with incomplete recording; and (III) occurrence of a prolonged interval, when the genetic correlation between growth and the underlying trait was 0.1. The leftmost points refer to an index weighting of 30; the rightmost points to .1.

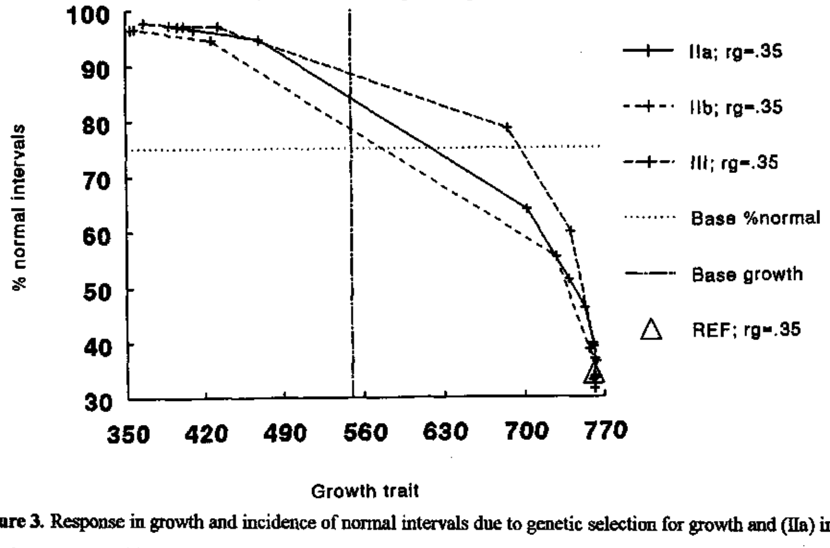

Figure 3. Response in growth and incidence of normal intervals due to genetic selection for growth and (IIa) interval from weaning to estrus with complete recording; (IIb) interval from weaning to estrus with incomplete recording; and (III) occurrence of a prolonged interval, when the genetic correlation between growth and the underlying trait was 0.35. The leftmost points refer to an index weighting of 30; the rightmost points to .1.

Table 3. Response in growth when the response in incidence of normal intervals is zero, for each of the strategies, obtained by interpolation.

	r_g=.1		r_g=.35	
	Response growth	Index weight	Response growth	Index weight
Reference (100%)	+213	-	+211	-
Strategy I	89%	n/a	0%[a]	n/a
Strategy IIa	92%	0.9	32%	3.1
Strategy IIb	92%	3.7	13%	7.5
Strategy III	95%	4.0	70%	9.0

[a] No interpolation possible; response in incidence of normal intervals always lower than zero.

Estimation of breeding values. BLUP breeding values were estimated using an animal model including all data and genetic relationships between animals. For strategy III, the approach of Janss and Foulley (1994) was followed to estimate breeding values for growth and the trait underlying the occurrence of a prolonged interval, which was scored as an all-or-none trait. Genetic parameters were either set to the values used for simulation (strategy I and III) or estimated from 10 separately simulated sets of data (strategy IIa and IIb), which were not included in the study (Table 2).

Results

The responses in growth and incidence of normal intervals for each alternative of strategy I are shown in Figure 1. The responses for strategy IIa, IIb and III, when the genetic correlation between growth and the underlying trait is .1 are shown in Figure 2, and the responses when the genetic correlation is .35 are shown in Figure 3. Indicated in these figures are also the incidence of normal intervals in the base generation (Base % normal), growth in the base generation (Base growth) and the responses in the reference situation (REF). For example in

Table 4. Average length of normal interval, prolonged interval, and interval from weaning to estrus for alternative index weightings of strategy IIa (in days)

	r_g=.1			r_g=.35		
	NORM	PROL	IWE	NORM	PROL	IWE
.1	5.7	18.2	10.1	5.7	17.2	12.8
.5	5.7	15.9	8.7	5.7	16.1	11.6
1	5.6	16.6	8.5	5.6	15.4	10.6
2	5.6	17.1	8.3	5.6	15.7	10.4
5	5.6	16.5	8.1	5.6	16.5	10.3
10	5.5	17.5	8.1	5.6	15.2	9.5
20	5.6	16.5	7.7	5.6	15.9	9.7
30	5.6	16.0	7.7	5.6	16.4	9.8

Figure 2 (r_g=.1), when the response in growth is 720 units, then for strategy III incidence of normal intervals is expected to be 86% on average. It appeared that strategy III always gave the best combination of response growth and incidence of normal intervals.

Table 3 shows the response in growth, relative to the response in the reference situation, when the response in incidence of normal intervals is zero. For both values of the genetic correlation, the response was highest for strategy III.

For strategy I it was allowed that the test capacity was not entirely used, when an insufficient number of sows was in estrus within the specified time period. For both r_g=.1 and r_g=.35, only culling after 7 d anestrus reduced the average number of tested animals per generation. Numbers of animals tested per generation were on average 475 and 471, respectively, instead of 480.

Average lengths of normal interval, prolonged interval and interval from weaning to estrus in generation 9 are shown in Table 4 for strategy IIa, in Table 5 for strategy IIb, and in Table 6 for strategy III. The average prolonged interval in the base generation was 28.0 d. Each strategy showed a decrease in average prolonged intervals, except for high index weights in strategy Iia, Iib and III. The negative genetic correlation between prolonged interval and

Table 5. Average length of normal interval, prolonged interval, and interval from weaning to estrus for alternative index weightings of strategy IIb (in days)

	r_g=.1			r_g=.35		
	NORM	PROL[a]	IWE[a]	NORM	PROL[a]	IWE[a]
.1	5.7	9.5	6.9	5.7	9.9	8.0
.5	5.6	9.8	6.8	5.6	9.8	7.9
1	5.6	9.6	6.6	5.6	9.9	7.6
2	5.5	9.8	6.4	5.6	9.8	7.3
5	5.4	10.3	6.1	5.3	10.2	6.7
10	5.2	10.5	5.9	5.2	10.4	6.4
20	5.0	10.7	5.6	5.1	10.6	6.1
30	5.0	10.7	5.6	5.0	10.6	5.8

[a] Only intervals up to 21 d measured

growth caused the direct (if any) and the correlated response in prolonged intervals to be downward, when the response in growth was positive. The correlated response in length of prolonged intervals was negative when the response in growth was negative. The response in prolonged intervals was smaller when index weights for the rebreeding trait in strategy IIb and III increased. This means that the response in length of prolonged intervals in these strategies was only due to the response in growth. This is evident for strategy III, because there was no selection pressure on prolonged interval. Apparently, with incomplete data (strategy IIb), the selection pressure moved from the length of prolonged intervals to the length of normal interval, when selecting for a short interval from weaning to estrus.

For high index weights of strategy III, the direct response in growth was smaller than the correlated response due to selection against prolonged intervals, because growth was impaired, compared to the level in the base generation. Consequently, the negative response in

Table 6. Average length of normal interval, prolonged interval, and interval from weaning to estrus for alternative index weightings of strategy III (in days)

	r_g=.1			r_g=.35		
	NORM	PROL	IWE	NORM	PROL	IWE
.1	5.7	17.8	10.4	5.7	18.0	14.2
.5	5.7	19.0	10.6	5.6	18.2	14.1
1	5.7	18.7	10.5	5.7	17.7	13.4
2	5.7	18.7	9.6	5.7	18.1	13.3
5	5.7	18.6	8.5	5.8	18.5	10.9
10	5.6	20.2	7.7	5.6	21.4	9.1
20	5.6	24.5	7.4	5.4	40.1	6.3
30	5.7	28.0	7.5	5.4	48.8	6.6

growth caused a negative correlated response in the length of prolonged intervals (Table 6). Increasing the index weight caused a decrease in length of interval from weaning to estrus, for each of the strategies. Average intervals from weaning to estrus shown in Table 5 are not directly comparable with those shown in Table 4 and 6, because intervals longer than 21 d were not recorded and therefore not included in the means in Table 5.

Discussion

Selection against incidence of prolonged intervals was most efficient by strategy III. Strategy IIa and IIb yielded similar responses for growth, but this was accompanied by a lower response in incidence of normal intervals. Strategy I showed a lower response than the other strategies for incidence of normal intervals.

In strategy I, breeding values were estimated in a univariate analysis, which was expected to yield a lower maximal response for growth, than a multivariate analysis. When genetic correlations deviate from zero, a multivariate analysis with appropriate model and parameters yields breeding values with improved accuracy, and a higher response (Pollak et al., 1984).

Univariate and multivariate analyses, however, were not different in this study (P > .05). Culling animals in addition to a univariate analysis of breeding values improved incidence of normal intervals, but decreased the response in growth substantially. Response in growth was not different for culling after 7, 14, 21 or 28 d (P > .05). Putting more progeny of the same highly ranking parents on test, as applied in strategy I, may increase the response in growth somewhat, but will also increase the rate of inbreeding.

Strategy IIa is in fact only a theoretical situation, for it is economically unattractive to measure intervals from weaning to estrus much longer than 3 or 4 wk. Strategy IIb, in which sows are culled after 21 d of anestrus, is a more feasible alternative. Breeding values were estimated here in a censored set of data, and culled animals, treated as a missing value, received a breeding value based on information of less extreme (because observed) relatives. This may cause some bias in estimated breeding values. The difference in responses between strategy IIa and IIb was only small. This may be due to the negative genetic correlation between growth and length of prolonged interval. Selection for growth reduced the average length of prolonged interval even when using strategy IIb, although information on the trait itself is largely absent.

Interval from weaning to estrus is a composite trait. There is some evidence that a change in incidence of normal intervals will cause genetic parameters of interval from weaning to estrus to change. Strategy IIa and IIb might have yielded better results, if genetic parameters were estimated every generation, although this may be difficult to realize, because of insufficient numbers of observations.

With strategy III, it looks as if a lot of information is ignored, because a continuous trait is transformed to a binary trait. Nevertheless, the binary trait is the trait to be improved, because we wish to reduce the incidence of the problem, rather than maintaining it and making it less serious. Using this method implies the assumption of one underlying trait causing prolonged intervals, which was fulfilled in this study, because we simulated it that way. This may not be the case in practice, so selection using strategy III might be less effective in practice than in this study. Further, in this study we used the true genetic parameters to estimate breeding values, but in practice, genetic correlations are extremely difficult to obtain for a binary trait and a continuous trait using an animal model. It means that in practice, we have to make a guess about these parameters. Hence, the response will be suboptimal if the assumed genetic correlation deviates from the 'true' genetic correlation. Nevertheless it is possible to estimate the heritability for the binary trait.

The clear favorable correlated response in length of prolonged interval due to selection for growth is awkward from a biological point of view. The favorable correlation between the two traits, obtained from Ten Napel et al. (1996b) and used for simulation, may be an artifact, caused by the existence of more than one underlying trait. If the genetic correlation would have been assumed unfavorable, then strategy IIb, but also strategy IIa, would probably have yielded poorer responses of selection. The responses for strategy III would not have been much different.

In this study all first-litter sows were replaced by gilts. This means that the number of observed intervals from weaning to estrus after the first parity is maximal, given the size of the herd. In practice, the number of observed intervals is reduced to 25 to 40% of the maximum, depending on the fraction of sows replaced. This means that in practice, less information is available for estimation of breeding values, or genetic parameters, and genetic progress in rebreeding traits will be lower than reported here.

The genetic correlations between the trait causing prolonged intervals and growth were set to .1 and .35 to compare the strategies. In reality, this genetic correlation is probably lower than .35 (Ten Napel et al., 1996b). If instead of an associated trait (such as growth in this study), a trait actually *causing* prolonged intervals is under selection, which for example might be the case when selecting for a high litter weaning weight in a lactation of given length, the genetic correlation may be as high as .35.

It is clear from this study that it is difficult to select against poor rebreeding performance. Selection on EBV's for the occurrence of a prolonged interval seems the most appropriate method to select against prolonged intervals, whilst maintaining the genetic progress in growth, if appropriate genetic parameters can be obtained. Selection on EBV's for the interval from weaning to estrus, estimated in a censored set of data, was also a feasible and successful method to decrease average interval from weaning to estrus in this study. Independent culling was inferior to the other strategies.

Acknowledgment

The authors would like to thank E. W. Brascamp, B. Kemp, T. van der Lende and J. K. Oldenbroek for discussion and reading of the manuscript.

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Appendix

To simulate an exponentially distributed variable (prolonged interval) that is genetically and residually correlated with a number of normally distributed variables, the following approach was used.

It was assumed that phenotypic values for prolonged interval for animal j followed the following distribution:

$$Y_{e,j} \cong f(x) = \frac{1}{\mu_{e,j}} * e^{\frac{1}{\mu_{e,j}}*(x-5)} \qquad [1]$$

where

$$\mu_{e,j} = \mu_e + u_{e,j} \qquad [2]$$

where μ_e is the over-all mean of the prolonged intervals, and $u_{e,j}$ is the additive genetic value of animal j for prolonged interval, which is assumed to follow a normal distribution. If the correlation structure between residuals should be taken into account as well, we can not generate a random sample from this distribution. Since we sample the additive genetic values and the residuals from multivariate normal distributions (4 traits), we have a normally distributed residual for prolonged interval, that has the appropriate correlation structure with the other traits. Because we know the mean and the variance, we can use this sampled residual to calculate the random number that was used to generate this residual. The random number follows a uniform distribution between 0 and 1. A phenotypic value is sampled from the

$$F_{inv} = 5 - \ln(1-x) * \mu_{e,j} \qquad [3]$$

distribution in [1] by substituting the calculated random number in which is the inverse of the cumulative density function of Y_e.

To study the properties of this method, we simulated 100 populations of 2400 animals (one generation), using the parameters shown in Table 1 of the paper, and averaged variance and covariance components, calculated from simulated additive genetic values, residuals, and phenotypic values. The calculated heritability for the exponential trait was somewhat lower than the one used for simulation (.12 vs .17), and genetic and residual correlations deviated less than .01 from the values used for simulation.

Chapter 8

General discussion

Jan ten Napel

Every characteristic that can be measured or recorded on a pig is the result of complex physiological processes. For the majority of characteristics, many genes are expressed, but the degree to which expression occurs through a given gene is determined by the interaction between the organism and its internal and external environment. Genes do not cause a trait but are templates for substances involved in the process of expression of the trait. Gene action is interactive in nature, but simulation studies, selection experiments and breeding programmes have shown that expression of many traits can be reasonably approached assuming an additive gene model (Keightly, 1989). Further, a pig must function as a whole, so it is likely that continuing changes in the processes of expression of a trait due to selection, affect expression of traits related to fitness, such that fitness is reduced if the environment of the pig is not adapted (Beilharz et al., 1993). Also, the environment can be subject to changes that reduce fitness if the pig is not adapted by genetic selection. In such cases, the genetic relationships between traits under selection and fitness traits are dependent on the genetic level for the traits under selection. It is necessary therefore, to examine and take into account the biological backgrounds when analysing responses of selection on a trait, instead of a priori assuming an additive gene model when analysing the trait.

Interval from weaning to estrus is determined by the start of cyclic activity and the incidence of a silent estrus, unnoticed either because badly observed or poorly expressed. If the start of the estrous cycle was blocked during lactation by suckling of the piglets only, the interval from weaning to estrus will be normal, i.e. a few days long, but if self-protecting mechanisms or abnormalities block follicular development as well, the interval from weaning to estrus will be prolonged. Thus, variation in the interval from weaning to estrus is determined by incidence of normal and prolonged intervals, variation in the length of normal intervals, variation in the length of prolonged intervals, and incidence of silent estrus (Chapter 2).

From studying distributions of intervals from weaning to estrus, it was established that intervals of 7 d or shorter can be considered normal, and other intervals prolonged (Chapter 3). For intervals from weaning to farrowing (that include interval from estrus to conception and gestation length as well) it was not possible to draw a line, because the overlap between the estimated distribution of normal intervals and the estimated distribution of prolonged intervals was too large (Chapter 4). In this case, probabilities of being a prolonged interval were assigned to intervals of a given length.

In the selection experiment described in Chapter 3, 5 and 6, the criterion of selection was a short interval from weaning to estrus. In fact, this selection procedure is essentially identical to selection against prolonged intervals, because the vast majority of sows in the selection line that were selected as a dam, had a normal interval from weaning to estrus. No response was observed in the length of either normal intervals, or prolonged intervals (Chapter 3), although genetic variation exists (Chapter 5). For prolonged intervals, the selection differential must have been nearly zero, because the majority of selected sows had only a normal interval, which is not informative for prolonged intervals (r_g=-.04). For normal intervals the genetic (and phenotypic) variation is very small, so the response becomes undetectable. There must have been a selection differential against silent estrus, but incidence of silent estrus was not reduced in the selection line, compared to the control line. This lack of response is likely due to absence of genetic variation, probably because the weekly relocation of sows was the main cause of silent estrus (Chapter 3). Thus, the achieved reduction in average interval from weaning to estrus in the selection experiment was only caused by a genetically decreased incidence of prolonged intervals.

This raises the question what caused the reduced genetic liability for a prolonged interval in the selection line. In Chapter 2 it was concluded that the liability for severe metabolic imbalance during lactation, and the liability for development of cystic ovaries are likely to be the major determinants of genetic variation in the liability for a prolonged interval. Metabolic imbalance can be a fast rate of body tissue loss prior to weaning, or depleted body reserves at weaning (Chapter 2). Many characteristics, such as voluntary food intake, milk production, litter size, and body reserves at farrowing may cause metabolic imbalance and initiate self-protecting mechanisms that block the final stages of follicular development.

Unfortunately not all of these characteristics were measured in the selection experiment, and incidence of cystic ovaries was not recorded either. Available were body condition score as a measurement of body reserves, both at farrowing and weaning, litter size at birth, and average daily gain in litter weight as a measure of milk production. None of these traits showed a significant response due to selection for a short interval from weaning to estrus. For all of the traits mentioned, estimated breeding values were different between sows with a normal and sows with a prolonged interval, in at least one line. As explained in Chapter 5, the observed contrast is an underestimation of the 'true' contrast, and selection for any of these traits will affect incidence of prolonged intervals more than selection against prolonged intervals will affect any of these traits.

Traits measured in the selection experiment that more or less reflect the traits selected for in commercial populations are average daily gain in the rearing pen, reflecting average daily gain in the test, and body condition score at moving to the mating pen as an approximate measurement of backfat depth at the end of the test. Only body condition score showed a small difference in estimated breeding value between sows with a normal and sows with a prolonged interval. None of the traits measured showed a genetic trend due to selection.

It is easier to find a genetic relationship between a trait and incidence of prolonged intervals in a population selected for that particular trait than in other populations (Chapter 5). In fact, this is the genetic relationship breeders are interested in, to be able to predict to what extent incidence of prolonged intervals is increased, as a correlated response of selection for economically important traits. In a set of data from an American commercial pig breeding company, consisting of four closed populations, inconsistent genetic relationships were found, when only data from sows with an observed interval from weaning to farrowing was included. After including data from sows that were culled after normally weaning the first litter as data from sows with a prolonged interval, genetic relationships were consistent and unfavourable in each of the four populations.

Although it is easier to find a genetic relationship between a trait and incidence of prolonged intervals in a population selected for that trait, one needs a selection experiment for every trait of interest, to study the genetic relationship with incidence of prolonged intervals. The size of such a selection experiment needs to be larger than the size of a similar experiment to study efficacy of selection on that trait, in order to have a sufficient number of animals with observed rebreeding performance after weaning the first litter. The number of observed intervals from weaning to estrus after the first parity is also the major limitation of using data from commercial breeding companies.

Excluding selection-line sows treated to induce puberty, from being selected as a dam, interfered with selection for a short interval from weaning to estrus. All treated gilts that farrowed in the experiment, responded to the treatment within a few days (otherwise they would have been excluded from the experiment, see Chapter 3). This means that they were not cycling at the time of treatment, although they were between 240 and 270 d old. From the principal component analysis in Chapter 6, it can be seen that treated gilts either performed poorly in the rearing pen, or were just young at entering the mating pen. Those that performed poorly were more likely to have a prolonged interval after weaning the first litter, but those that were just young were not. Apparently, in the former group, continued follicular development was blocked because of metabolic self-protecting mechanisms. Since a metabolic block of follicular development is less common in older sows than in first-parity sows, even with similar amounts of body weight loss, it may be that those self-protecting mechanisms block development of follicles sooner if the need to gain essential body tissue (muscles, organs) is higher, which is normally a function of age.

Strategies to select against poor rebreeding performance whilst maintaining genetic gain in the economically important traits were compared in a simulation study. Independent culling was less effective in reducing incidence of prolonged intervals, than the other strategies. Selection on estimated breeding values of occurrence of a prolonged interval, using a threshold model, was the most efficient strategy. Selection on estimated breeding values for the interval from weaning to estrus was effective in reducing the average interval from weaning to estrus, even when only intervals up to 21 d were observed (Chapter 7).

We used estimates of genetic parameters from Chapter 5 and 6 for simulation of data. The fact that we included the unexpectedly favourable genetic correlation between the growth trait and the length of the prolonged interval is to some extent responsible for the favourable result of selection on estimated breeding values of interval from weaning to estrus.

In the simulation study we estimated breeding values for occurrence of a prolonged interval using a threshold model in a multivariate analysis. We used the genetic correlation as used for simulation of data. In practice, this genetic correlation is extremely difficult to estimate. It is possible to do two univariate analyses instead of a multivariate analysis, because the heritability of the trait supposedly underlying the occurrence of a prolonged interval can be estimated (Chapter 5), but an estimate for the genetic correlation is still needed for combining the two breeding values in a selection index.

In conclusion, incidence of prolonged intervals shows genetic variation, and it is unfavourably genetically related with economically important traits that are generally selected for in current breeding programs. Incidence of prolonged intervals can be reduced by genetic selection.

Literature Cited

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In general, sows do not ovulate or show estrus during lactation. In normal conditions a sow shows estrus between 4 and 7 d after weaning. Especially among first-litter sows, however, the time from weaning to estrus is highly variable, and may be 200 d or longer. The aim of this thesis was to study whether the high variability in rebreeding performance has a genetic basis, whether poor rebreeding performance is genetically related to economically important traits, and whether it is possible to reduce the genetic liability for poor rebreeding performance.

Interval from weaning to estrus consists of interval from weaning to start of cyclic activity, interval from start of cyclic activity to estrus, and an estrous cycle length if the first estrus is not observed or expressed. From reviewing literature it was concluded that variation in interval from weaning to estrus is determined by the interval from weaning to the start of the cycle, and the incidence of silent (i.e. unnoticed) estrus. Normally, weaning is the start of cyclic activity, because the lactational block of follicular development is relieved, but if other conditions, such as weight loss or stress block follicular development as well, the interval from weaning to the start of cyclic activity is non-zero and highly variable. Therefore, it is proposed to distinguish normal and prolonged intervals from weaning to estrus (Chapter 2).

Analysis of a selection experiment on a short interval from weaning to estrus showed that genetic variation in intervals from weaning to estrus is substantial (h^2=.36 ± .05), and genetic selection for a short interval from weaning to estrus was effective. The selection applied appeared to have increased the number of sows with a normal interval, instead of changing the average normal or the average prolonged interval. Incidence of silent estrus was not different between the selection line and the control line (Chapter 3).

Genetic relationships between rebreeding performance and other traits were studied in two ways; with data from a population of a commercial breeding company selected for high average daily gain and low backfat, and with data collected in the selection experiment. Intervals from weaning to estrus or farrowing were transformed to the probability that the interval was prolonged. For interval from weaning to estrus the resulting trait was a binary trait. Estimation of an unbiased genetic correlation between a binary and a continuous trait is very difficult, so instead genetic relationships were studied by comparing means of estimated breeding values of sows with a normal interval with those of sows with a prolonged interval for each of the continuous traits.

Analysis of the data from the population selected for daily gain and against backfat showed no clear genetic relationships with incidence of prolonged intervals from weaning to farrowing, when only sows with an observed interval were included. An additional analysis was done taking into account that part of the sows were culled because of anestrus. Sows that were culled after normally weaning a litter were supposed to be culled for anestrus, and included in the analysis as having a prolonged interval. In this second set of data, genetic relationships between rebreeding performance and the traits under selection were now mostly significant and consistently unfavourable (Chapter 4).

Analysis of traits measured on the sow and her litter in the selection experiment revealed no trends due to selection for any of the traits measured. Body condition traits and litter traits, except number of pigs dead during lactation, showed a significant unfavourable genetic relationship with incidence of prolonged intervals from weaning to estrus in at least one line. It is shown that the fact that a prolonged interval has a wide range of possible causes makes it extremely difficult to prove the existence of each of these causal relationships. Also due to the many possible causes, use of genetic correlations will cause underestimation of the expected correlated response in rebreeding performance due to selection for economically important traits. Further, it was observed that the liability for a prolonged interval was higher when a sow was treated with exogenous hormones to induce puberty (Chapter 5).

Analysis of traits measured during rearing in the selection experiment showed than none of these traits had changed due of the selection applied. Further, none of these traits showed a genetic relationship with incidence of prolonged intervals (Chapter 6).

Strategies to select against poor rebreeding performance were compared in a simulation study. We simulated 120-sow nucleus unit with selection practised for 9 generations. There was one economically important trait, which was subject to selection and which was unfavourably correlated with a trait causing prolonged intervals (r_g=.1 and r_g=.35). The three strategies were independent culling (I), selection on estimated breeding values for interval from weaning to estrus (II) and selection on estimated breeding values for occurrence of a prolonged interval (III). Selection against poor rebreeding performance appeared to be difficult. Selection strategy III was in this study the most appropriate method, and strategy II was also a successful method to decrease average interval from weaning to estrus, even when sows were culled for anestrus at 21 d after weaning. Strategy I was inferior to the other strategies (Chapter 7).

In conclusion, interval from weaning to estrus is heritable and improvement by genetic selection is feasible. Interval from weaning to estrus or farrowing is a mixture of normal and prolonged intervals from weaning to estrus. Incidence of prolonged intervals is a major contributor to genetic variation in interval from weaning to estrus. Genetic selection for improved growth rate, decreased backfat, and increased litter size and litter weight may cause an unfavourable correlated response in incidence of prolonged intervals.

Curriculum vitae

Jan ten Napel werd op 10 april 1966 in Ermelo geboren. Na de lagere school ging hij in 1978 naar de Gereformeerde Scholengemeenschap Amersfoort. In 1984 behaalde hij daar het Atheneum-B diploma, waarna hij naar de Christelijke Agrarische Hogeschool "De Drieslag" in Dronten ging. Deze opleiding rondde hij in 1988 af met het behalen van het diploma Nederlandse Landbouw, specialisatie Melkveehouderij. Na vervulling van de militaire dienstplicht begon Jan in 1989 aan het doorstroomprogramma Zoötechniek van de Landbouwuniversiteit in Wageningen. Tijdens zijn studie werkte hij twee keer twee maanden als onderzoeksassistent bij het IVO-DLO "Schoonoord" in Zeist, en vier maanden als docent Statistiek. In november 1991 studeerde hij met lof af, met als hoofdvak Veefokkerij, waarna hij werd aangesteld als Assistent in Opleiding bij dezelfde vakgroep, en gedetacheerd bij het IVO-DLO. Sinds november 1995 werkt Jan bij JSR Healthbred Ltd. in Southburn (East Yorkshire) in Groot Brittanië als fokkerijdeskundige.