Snow shoes and sandals?

Genetic aspects of heat stress sensitivity and sow reproduction

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Abstract

Globally the average size of pig herds are increasing and amount of labour spent per sow / finisher pig is decreasing. These changes require sows which need less management interventions. In addition to easier manageable sows modern genotypes will also need to be more adaptable considering that global temperatures are expected to increase and pork production is partially moving to warmer climates. The end result is that commercial pigs nowadays will potentially face more heat stress challenges during their productive lives.

In this thesis, a model was developed which was used to estimate upper critical temperatures for sows' reproductive performance. Additionally the possibility to breed for reduced heat tolerance of sows was investigated. Therefore heritability for the random regression slope of farrowing rate against increasing temperature at day of insemination (= heat tolerance) and the genetic correlation between farrowing rate and heat tolerance was estimated. Commercial production pigs are crossbreds farmed all over the world. In contrast, selection is practiced mainly in temperate climates, in nucleus herds using purebred pigs. The success of genetic selection depends on how much genetic progress is realized in crossbred pigs. Within this thesis these genetic correlations for farrowing rate between purebreds and crossbreds were estimated.

Sow productivity depends on a number of related traits, such as ovulation rate, the number of litters per sow per year, the number of weaned piglets per sow per year, and the length of productive live. Traditionally pig breeding programs have improved sow productivity by increasing number weaned piglets per sow per year. To improve herd-level litters per sow per year a new trait was proposed called problem free sow production by parity, which incorporates the traits interval weaning first insemination, non-return rate, farrowing rate, and selection for next parity. Heritability of problem free sow production and genetic correlations with other sow production traits were estimated.

The main conclusion of this thesis was that it is possible to select for improved heat resistance in addition to improved commercial production levels in commercial pigs. However, genetic correlation between production in temperate and hot climates is high. This high correlation implies that, within-line, pigs with the best performance in a hot climate will be the best in temperate climate too. Most important for the success of a pig breeding program is to define appropriate breeding goals which are based on the environment(s) that market pigs are expected to perform in. The overall data collection for the genetic evaluation needs to be done in those specific environments and this will favour pigs which are able to produce over more than one specific environment.

Abbreviaton key

CCPS: combined crossbred-purebred selection
D-line: Dutch Yorkshire line
FR: farrowing rate
ILW-line: International Large White line
LS: litter size (= total born)
PFSP: problem free sow production
RC: reciprocal cross
TB: total born (= litter size)
TNBF: total number born from first insemination
UCT: upper critical temperature

Dam line(s) = sow line(s) and vice versa

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1

General introduction

1.1 Introduction

Genetic potential of commercially bred pigs has improved during the past 50 years as a result of well-organized breeding programs. This improved genetic potential has led to improvement of economical important traits such as back fat thickness, daily gain, feed efficiency, and litter size (Merks, 2000; Brown-Brandl et al., 2004). Implementation of crossbreeding, specialized sire and dam line breeding, and BLUP genetic evaluation programs have been responsible for a remarkable reduction of back fat (-75%), improvement in growth rate (+100%), and since the 1990s in larger litter sizes (+25%) (Merks et al., 2012). Since the turn of the century, breeding goals within modern pig breeding programs have shifted more towards improving product quality as well as to traits related to animal welfare such as piglet survival, finisher survival, sow longevity, and disease resistance (Kanis et al., 2005).

1.2 Trends in pork industry

Globally the average size of pig herds is increasing and amount of labour spent per sow/finisher pig is decreasing (Eurostat, 2010). This requires sows which need less management intervention and which are easier to manage on a daily basis. At the same time, the human population size is growing. Meat demand and with that production is therefore expected to double from 229 million tonnes in 1999 to 465 million tonnes in 2050, the growth is predicted to be the fastest in regions such as Latin America and South and East Asia which are characterized by hotter climates (FAO, 2006) and generally a lower standard of available pig accommodations. Furthermore, the temperature is expected to increase worldwide as a result of climate change (Hofmann, 2010). Economic losses from heat stress in the swine industry have been estimated to be $299 million a year in the United States. These costs are mainly a result from an increased number of open (non-productive) days for sows and reduced growth rates for finishers (St-Pierre et al., 2003).

1.3 Sow production efficiency

Historically the focus of dam line pig breeding programs was primarily on increasing litter size (Dekkers et al., 2011). Sow productivity however depends not only on litter size, also litters per sow per year and length of productive life are important. From an economic perspective for large industrial agricultural enterprises however the metric of increasing litters per sow per year is the most interesting parameter. Non-productive days in which a sow is neither gestating nor lactating include days between weaning and insemination, lost days from an unsuccessful gestation, failed conception, abortion, and death (Wilson et al., 1986). During these days the sow is not generating profit and only costing the overall system revenue. The cost of one non-productive sow day has been estimated to be around €2.20 in the Netherlands (Wageningen Livestock Research, 2011) and includes the cost of feed, building, and loss in piglet production. Globally on average more than 10% of the sows do not farrow from first insemination and return to estrus (PigCHAMP 2010a; PigCHAMP 2010b; Kengetallenspiegel, 2011). This directly affects number of litters per sow per year and non-productive sow days. Reduction of these non-productive days will result in an improved number of litters per sow per year and therefore to an improved herd productivity and at the end in more profit. Finally, it should also be noted that the sow provides 50% of the potential finisher pig genetics and thus one should have a balanced breeding goal not only based on sow productivity but also on traits of economic importance in the finisher pig. However, the traits important to the potential finisher are not discussed in the context of this thesis as the focus is on sow reproductive efficiency.

1.4 Pigs and heat stress

As the temperature is expected to increase worldwide with 1.8°C to 4.0°C in the next 90 years (FAO, 2006) and pork production is partially moving to warmer climates, commercial pigs could potentially face more heat stress challenges during their productive life. Pigs are highly sensitive to elevated ambient temperatures because they cannot sweat and have problems regulating their internal temperature through increased respiration or panting. Pigs suffer from heat stress when temperature exceeds the upper critical temperature of their thermo-neutral zone. The thermo-neutral zone is the range of ambient temperatures between the lower critical temperature and the upper critical temperature (Bianca, 1976). This zone has been shown to lie between 12°C and 22°C for lactating sows (Black et al., 1993). Below the lower critical temperature pigs experience cold stress. Pigs suffering from cold stress increase their internal heat production by shivering or by increasing their feed intake. This increased feed intake is mainly used to raise the body temperature through an increased metabolic rate rather than to increase production, i.e. growth rate (Quiniou et al., 2001). Above the upper critical temperature pigs suffer from heat stress. Pigs have various physiological processes to cope with heat stress. Through radiation, conduction, convection, and evaporation pigs can transfer heat from their body to their environment. Wild pigs suffering from heat stress in their natural habitat, regulate their body temperature by wallowing in mud or water and become increasingly nocturnal (Bracke, 2011). In the modern pig industry mud or water for wallowing is not available and pigs have to cope with their given environment. To compound the issue of heat stress, it has also been shown that the internal heat production of pigs has increased during the past 50 years due to increase in leanness (Brown-Brandl et al., 2004). Higher internal heat production lowers heat tolerance capacity, resulting in increased susceptibility to heat stress (Brown-Brandl et al., 2001). Heat stress is expressed in an increased rectal temperature, respiration rate, skin temperature, and heat production (Omtvedt et al., 1971). The rectal temperature increases with initial exposure to heat stress, but gradually decreases with length of exposure to heat stress (Omtvedt et al., 1971). Next to physiological changes due to heat stress, heat stress also influences performance. In general, heat stress affects fitness traits i.e., an animal's ability to produce and reproduce. In pig production this relates mainly to reproduction.

1.5 Breeding and environmental sensitivity

In major pig breeding organizations, selection takes place in nucleus farms in mainly temperate climates and under high management standards (Knap, 2005). Selection on production solely based on data from improved environmental conditions leads to increased environmental sensitivity (Van der Waaij, 2004). During recent years the number of pig breeding programs has been reduced and it is expected that until 2020 there will only be further consolidation. This leads to a small number of pig breeding companies producing pigs for many different environments (Gibbs et al., 2009; Dekkers et al., 2011; Merks et al., 2012). These environments differ in altitude, temperature, feed quality, health status and pig management. As a result the pigs of the future will have to be able to produce within a multitude of differing environments.

1.6 Aim and outline of the thesis

Heat stress is expected to have negative effects on sow production and amount of labour per sow is expected to reduce, therefore the overall objective of this thesis is to improve understanding of the genetic aspects of heat stress sensitivity, ease-of-management traits, and sow reproductive performance. The first aim in this thesis will be to compare two dam lines (a Yorkshire dam line and a Large White dam line) for their differences in heat tolerance as measured by differences in their reproductive performance. It is hypothesized that there is a lower and upper critical temperature for sow performance and this could differ per line. To test this hypothesis, plateau linear models will be used to estimate upper critical temperatures for farrowing rate and total born for both dam lines. Above the thermo-neutral zone the decrease in farrowing rate and total born per degree Celsius will be estimated for both dam lines (Chapter 2). Fertilization and maintaining gestation in warm and hot climates is a challenge, but even in temperate climates fertilization is valuable because of potential reduction of number of non-productive sow days. Genetic variation for farrowing rate of sows from the two dam lines and their reciprocal cross will be estimated to determine if genetic selection on farrowing rate might be possible. To then to be able to genetically improve farrowing rate under high temperatures, there is a need to find genetic variation. Therefore, heritability for the random regression slope of farrowing rate against increasing temperature at day of insemination and the genetic correlation between farrowing rate and heat tolerance will be estimated (Chapter 3). The breeding goal in pig breeding programs is crossbred reproductive performance; however genetic selection is performed on purebred level. To understand the impact of improving crossbred traits on pure line animals crossbred models will be used to determine if pigs ranked best as purebreds for farrowing rate and heat tolerance are also breeding the best crossbreds (Chapter 3). In Chapter 2 and Chapter 3 only the effect of heat stress of day of insemination on reproductive performance is considered. However, it can be postulated that heat stress before or after day of insemination will also have a significant impact on reproductive performance. Therefore the most heat stress sensitive periods during the reproduction cycle need to be identified (Chapter 4) so that genetic models for heat tolerance can be optimized. To optimize sow efficiency and productivity and reduce the number of non-productive sow days a potential new trait called problem free sow production will be proposed. This trait will incorporate several traits related to ease of management. Genetic variation for problem free sow production in temperate and heat challenged conditions and genetic correlations with other sow reproduction traits will be estimated (Chapter 5). Finally, in Chapter 6 future implications for pig breeding programs as a result of changes in the global pork industry based on current trends and genetic adaptability of sows will be discussed.

2

Sow line differences in heat stress expressed in reproductive performance traits

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Abstract

The objectives of this study were 1) to investigate if there were differences in the relation between temperature and reproductive performance traits in two different sow lines, a Yorkshire line producing mainly in temperate climates and a Large White line producing mainly in warm climates, and 2) to determine the upper critical temperature (UCT) for the reproductive performance of these two lines. Sows are exposed to heat stress when temperature exceeds the UCT of the thermo-neutral zone. Data included 32,631 observations on reproductive performance from 11,935 sows on 20 farms in Spain, collected from 2003 to 2005. Sows belonged to two different purebred sow lines, named D (Yorkshire sow line, producing mainly in temperate climates) and ILW (Large White sow line, producing mainly in warm climates). Only first insemination records per parity were used and were combined with the maximum outside temperature at day of insemination. Upper critical temperatures were studied for three reproduction traits: farrowing rate (0 or 1), litter size (range from 1 to 25), and total number of piglets born per first insemination (combination of farrowing rate and litter size, range from 0 to 25). Data were corrected for fixed effects, which included parity, service sire, and an interaction between farm and year. Corrected data were used as observations in the models to study the effect of outside temperature on reproductive performance. Two models were compared for goodness of fit: a linear regression model and a plateau-linear model with the plateau representing the thermo-neutral zone and a linear decrease above that zone. Farrowing rate of ILW-line sows was not affected by temperature. For litter size and total number born per first insemination of ILW-line sows no UCT could be estimated. These traits were linearly affected by temperature. For all three reproduction traits of the D-line the best model was the plateau-linear model; the UCT for the D-line sows was estimated to be 19.2°C for farrowing rate, 21.7°C for litter size, and 19.6°C for total number born per first insemination. The decrease in reproductive performance of ILW-line sows with increasing outside temperature was less than in D-line sows. From this study it can be concluded that there are differences in heat stress tolerance between sow lines as measured by the differences in reproductive performance. These differences are an indication of genetic differences in heat stress tolerance in sow lines.

Key words: heat stress, reproductive performance, sow, sow line, upper critical temperature

2.1 Introduction

Reproductive performance in sow lines is of great importance in current commercial pig breeding programs (Hanenberg et al., 2001). It is affected by several factors such as breed, parity, lactation length, nutrition, season, and temperature. Several authors described an adverse effect of high temperature on reproduction (Peltoniemi et al., 1999; Tummaruk et al., 2004; Suriyasomboon et al., 2006). Sows are exposed to heat stress when temperature exceeds the upper critical temperature (UCT) of the thermo-neutral zone of the sow. This zone lies between 12˚C and 22˚C (Black et al., 1993) for lactating sows.

Pig production occurs on commercial farms all over the world including hot climates. Genetic selection of pigs for increases (re)production occurs in nucleus herds in mainly temperate climates. As a consequence, pig breeders face a wide variety of environmental conditions in which their pigs are required to perform (Knap, 2005). When evaluating breeding goals for dam lines, we were confronted with differences in appreciation of two sow lines by farmers in the Netherlands (a temperate climate) and in Spain (a warmer environment). The line preferred by Dutch farmers was not preferred by the Spanish and vice versa. Reproduction differences between Dutch and Spanish farms substantiated this opinion. In dairy cattle sufficient genetic variation has been found in heat stress tolerance for milk, fat, and protein production and non-return rate to allow selection (Ravagnolo and Misztal, 2000, 2002). To our knowledge no study has focused on the genetic variation in heat stress tolerance in sows.

The objectives of our study were 1) to investigate if there were differences in the relationship between temperature and reproductive performance traits in two different sow lines, a Yorkshire line producing mainly in temperate climates and a Large White line producing mainly in warm climates, and 2) to determine the UCT for the reproductive performance of these two lines.

2.2 Material and methods

Animal Care and Use Committee approval was not required for this study because data came from an existing database.

Data

Data were composed of 39,038 first insemination records from 12,442 sows inseminated from January 2003 until December 2005. Sows were kept on 20 sow farms in Spain; 2,850 sows originated from a Dutch (**D**) purebred Yorkshire sow line and 9,592 sows originated from an International purebred Large White sow line (**ILW**). Both sow lines belonged to genetic lines of the TOPIGS breeding company

(Vught, The Netherlands). For the ILW-line a nucleus farm with related multiplication farms was operated for more than 15 years in Spain. The nucleus farm provided its own female replacements; male replacements came from the Netherlands. Similar structures existed for Italy, the Philippines and Brazil. Data for EBV estimation came from all of these farms. For the D-line a similar structure existed over these years with solely Dutch nucleus and multiplication farms. Selection in both lines was based on daily gain, back fat, litter size and litter mortality. In Spain the D-line was located on 8 farms and the ILW-line on 12 farms.

In this study only first insemination results per parity were considered. Sows ranged in parity from 1 to 14. For each sow, sow identification number, birth date, parity, farm, sow line, first insemination date, service sire, and farrowing rate were available. For the sows that farrowed from first insemination, gestation length, farrowing date, litter size (**LS**), number of live born piglets, number of stillborn piglets, number of mummified piglets, and weaning date were available.

Farrowing rate (**FR**) was recorded as a binomial trait, with an underlying normal variation. It was defined as 1 if the first insemination resulted in a pregnancy and gestation length was longer than 108 days or if litter size was at least 1; otherwise, FR was defined as 0. Litter size was recorded immediately after farrowing and was defined as the sum of number of live born piglets, number of stillborn piglets, and number of mummified piglets. For sows which did not farrow from first insemination LS was missing. Litter size ranged from 1 to 25. Total number of piglets born per first insemination (**TNBF**) was defined by multiplying FR with LS. Therefore, TNBF was equal to LS when the sow farrowed from first insemination, and TNBF was defined as 0 when first insemination did not result in a farrowing. Thus, TNBF ranged from 0 to 25.

Meteorological data were obtained from the European Climate Assessment Dataset (Klein Tank et al., 2002) and included daily summaries for the maximum outside temperature for 7 Spanish weather stations and were available for the years 2003, 2004, and 2005. Each farm was assigned to the nearest weather station. Most of the farms had a weather station within 70 km of the farm, with the least separation being 3 km and the greatest separation being 160 km. Freitas et al. (2006) estimated a correlation of 0.9 between on-farm weather data and weather station data even for weather stations more than 300 km away from the farm. Each insemination record in our dataset was assigned the daily maximum temperature on day of insemination from the nearest weather station.

Observations with unknown maximum outside temperature at day of insemination were removed, reducing the dataset to 38,466 observations. In a preliminary graphical analysis of the data, 10°C seemed to be the lower critical temperature of the thermo-neutral zone (data not shown). Therefore, observations with a maximum outside temperature below 10°C were removed from the dataset. Due to a low number of observations with a maximum outside temperature at day of insemination exceeding 36°C, these observations were also excluded from the dataset.

The final dataset consisted of 32,631 observations from 11,935 sows on 20 farms with 2,759 D-line sows and 9,176 ILW-line sows.

Statistical Analysis

The descriptive analysis was performed for the D-line and the ILW-line separately using the MEANS procedure (SAS Inst. Inc., Cary, NC). For the descriptive analysis maximum outside temperature was divided into 27 temperature classes (10°C, 11°C, …, 36°C).

To test the effect of maximum outside temperature at day of insemination on reproductive performance, data were analyzed for the D-line and ILW-line separately using a two-step approach. First, data were corrected for systematic effects using the GLM procedure (SAS Inst, Inc) with the model:

$$y_{ijkl} = \mu + p_i + s_j + hy_k + e_{ijkl} \qquad (1)$$

where y_{ijkl} is the value of FR, LS, or TNBF, p_i is the effect of parity i (14 classes), s_j is the effect of service sire j (383 classes), hy_k is the effect of herdyear k (56 classes) and e_{ijkl} is a random residual term.

Corrected observations (y^*) for FR, LS, or TNBF were calculated for each insemination record as $y^* = \hat{\mu} + \hat{e}_{ijkl}$.

Second, corrected observations y^* were used to investigate the effect of temperature on FR, LS, and TNBF. To test whether there was a thermo-neutral zone and an UCT, two models were defined: a linear regression model and a plateau-linear model including a thermo-neutral zone (i.e., a plateau). For each sow line both models were tested for goodness of fit using the NLIN procedure (SAS Inst. Inc). The linear regression model was:

$$y_i^* = i + b * x_i + e_i \qquad (2)$$

where y_i^* is the corrected observation for FR, LS, or TNBF; i is the intercept; x_i is the maximum outside temperature at day of insemination varying from 10 to 36°C; b is the slope of y^* when x increases by 1°C (Figure 2.1); and a random residual term, e_i.

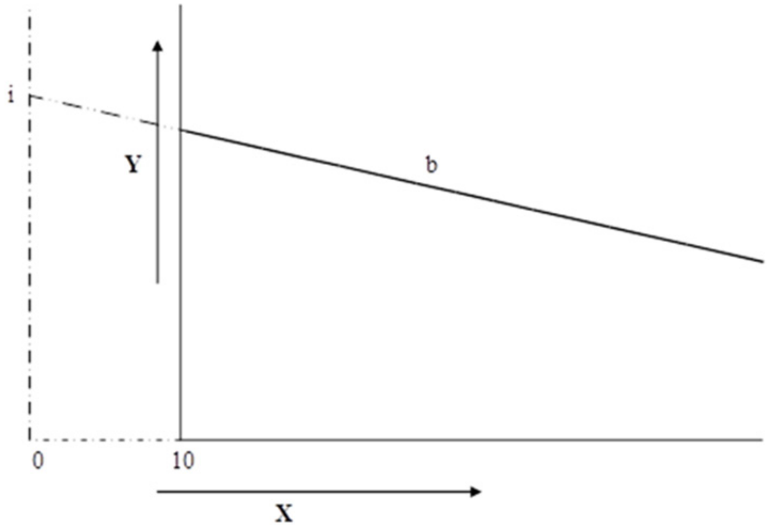


Figure 2.1 The linear regression model. X is maximum outside temperature at day of insemination, y is the corrected observation of the analyzed reproductive performance trait, i is the intercept, b is the slope of the decrease in y when x increases with 1 ˚C.

Subsequently, the linear regression model was adapted to the thermo-neutral zone theory by adding a plateau to the linear regression model resulting in a plateau-linear model. This concept describes the relationship between trait and temperature:

$$UCT = \frac{c-i}{b} \tag{3}$$

$$y_i* = c + e_i \text{ when } x_i \leq UCT \tag{4}$$

$$y_i* = i + b * x_i + e_i \text{ when } x_i > UCT \tag{5}$$

The first part of the concept estimates the *UCT* (3) of the thermo-neutral zone of the sow, where *c* is the constant value of y_i* when reproductive performance of the sow is unaffected by temperature; *i* is the intercept; and *b* is the slope of the decrease in y_i* when y_i* was affected by temperature (Figure 2.2).

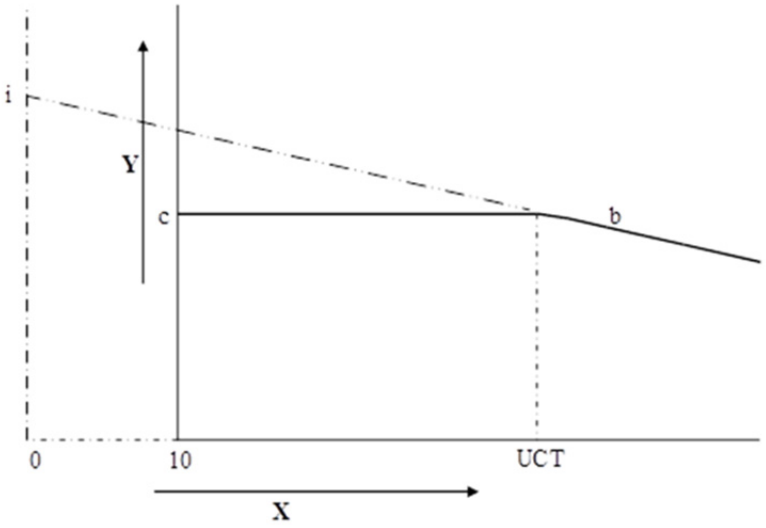


Figure 2.2 The plateau-linear model. X is maximum outside temperature at day of insemination, y is the corrected observation of the analyzed reproductive performance trait, UCT is the upper critical temperature, c is the constant of y when y is unaffected by temperature, i is an estimated value of y when temperature is 0˚C, b is the slope of the decrease in y when temperature increases with 1˚C.

In the second part of the concept the reproductive performance of the sow is unaffected by temperature (4), where y_i* is the corrected observation for FR, LS, or TNBF; *c* is the constant value of y_i* when reproductive performance of the sow is unaffected by temperature; e_i is the random residual term; and x_i is the value of maximum outside temperature at day of insemination (Figure 2.2).

The third part of the concept estimates the decline in reproductive performance when temperature exceeds the UCT (5): where y_i* is the corrected observation for FR, LS, or TNBF; *i* is the intercept; *b* is the slope of the decrease in y_i*; x_i is the value of maximum outside temperature at day of insemination; and e_i is the random residual term (see also Figure 2.2). Solutions for (3), (4), and (5) were generated iteratively.

An F-test was used to test per trait per line the fit of the plateau-linear model compared to the linear regression model.

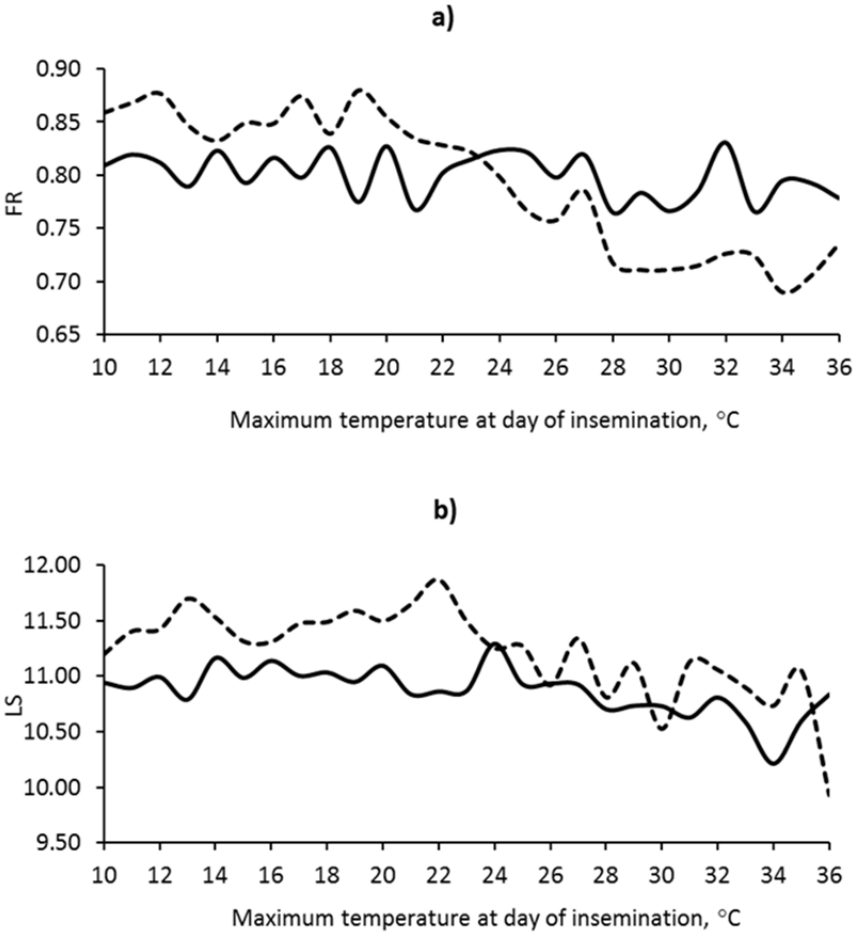
2.3 Results

Descriptive statistics of the data are presented in Table 2.1. Mean parity in the D-line (3.4) was slightly greater than in the ILW-line (3.2). Farrowing rate was equal in both lines, but D-line sows had greater mean LS than ILW-line sows. This resulted in a mean TNBF that was greater in the D-line (9.0) than in the ILW-line (8.7). Sows of the D-line were inseminated at days with, on average, a slightly greater maximum outside temperature than sows of the ILW-line: 22.4°C compared to 21.8°C (Table 2.1).

Means for FR, LS, and TNBF, graphed against maximum temperature at day of insemination, are shown in Figure 2.3. For temperatures below 23°C the FR, LS, and TNBF of sows of the D-line was greater than the FR, LS, TNBF of sows of the ILW-line. Above 24°C LS was approximately the same in the ILW-line and the D-line, but FR and TNBF were greater for the ILW-line when temperature exceeded 25°C (Figure 2.3).

Table 2.1 Number of observations (n), mean (avg), standard deviation (SD), minimum (min.), and maximum (max.) of seven reproductive performance traits and maximum outside temperature at day of insemination for two sow lines, a Dutch purebred Yorkshire line (D) and an International purebred Large White line (ILW).

	line	n	avg	SD	min.	max.
Parity number	D	7,573	3.4	2.3	1	14
	ILW	25,058	3.2	2.0	1	12
Gestation length (days)	D	6,138	113.4	7.5	100	123
	ILW	20,339	113.1	6.5	100	124
Farrowing rate	D	7,573	0.8	0.4	0	1
	ILW	25,058	0.8	0.4	0	1
Litter size	D	6,035	11.3	2.8	1	25
	ILW	20,051	10.9	3.1	1	24
Number born alive	D	5,963	10.5	2.7	1	20
	ILW	19,952	10.0	3.0	1	22
Number stillborn	D	1,960	2.5	2.0	1	16
	ILW	7,665	2.1	1.6	1	16
Total number piglets born per first insemination	D	7,573	9.0	5.2	0	25
	ILW	25,058	8.7	5.2	0	24
Maximum outside temperature at day of insemination (°C)	D	7,573	22.4	7.3	10	36
	ILW	25,058	21.8	7.5	10	36


a)
0.90
0.85
0.80
0.75
0.70
0.65
FR
10
12
14
16
18
20
22
24
26
28
30
32
34
36
Maximum temperature at day of insemination, °C
b)
12.00
11.50
11.00
10.50
10.00
9.50
LS
10
12
14
16
18
20
22
24
26
28
30
32
34
36
Maximum temperature at day of insemination, °C

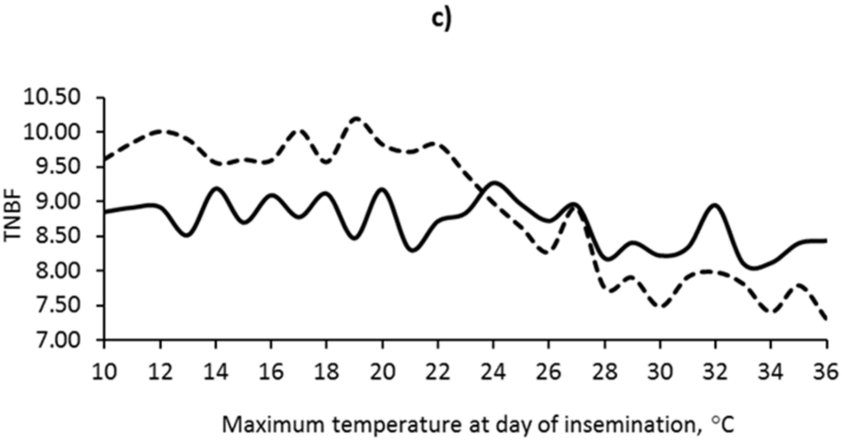


Figure 2.3 Means for three reproductive performance traits (a = farrowing rate (FR); b = litter size (LS), c = total number piglets born per first insemination (TNBF)) by maximum outside temperature at day of insemination, for two sow lines, a Dutch purebred Yorkshire line (- - -) and an International purebred Large White line (—).

Table 2.2 shows the results of the goodness of fit tests for FR, LS, and TNBF when testing no effect of temperature on reproduction versus a linear effect of temperature on reproduction, no effect of temperature on reproduction versus a plateau-linear effect of temperature on reproduction, and a linear effect of temperature on reproduction versus a plateau-linear effect of temperature on reproduction.

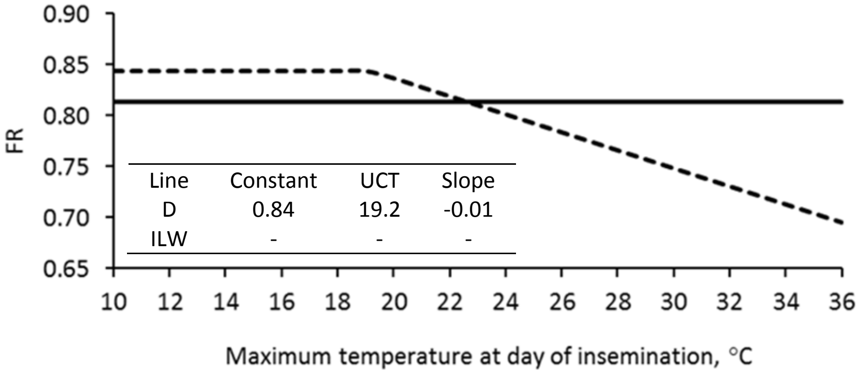
Table 2.2 Significance tests for linear (L) and plateau-linear (P) relations between three reproductive performance traits and maximum outside temperature at day of insemination for two sow lines, a Dutch purebred Yorkshire line (D) and an International purebred Large White line (ILW).

Reproduction trait	line	model	F_{model}[1]	P_{model}[1]	$F_{g.o.f.}$[1]	$P_{g.o.f.}$[1]
Farrowing rate	D	L	99.6	<0.01	12.5	<0.01
		P	56.1	<0.01		
	ILW	L	3.6	0.06		
		P	2.7	0.07		
Litter size	D	L	41.3	<0.01	4.7	0.03
		P	23.0	<0.01		
	ILW	L	17.3	<0.01	0.5	0.48
		P	8.9	<0.01		
Total number piglets born per first insemination	D	L	136.1	<0.01	15.5	<0.01
		P	75.9	<0.01		
	ILW	L	16.0	<0.01	1.9	0.17
		P	8.9	<0.01		

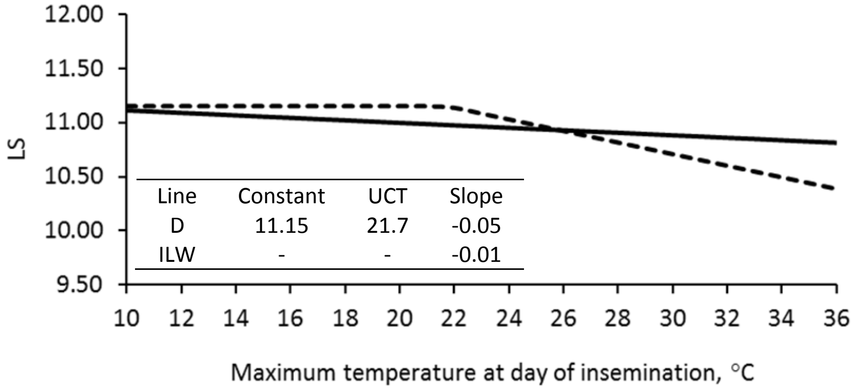
[1] F_{model}= F-value of the model; P_{model}= P-value of the model; $F_{g.o.f.}$= F-value of the goodness of fit test of the plateau-linear model (P) compared to the linear model (L); $P_{g.o.f.}$= P-value goodness of fit test of the plateau-linear model (P) compared to the linear model (L).

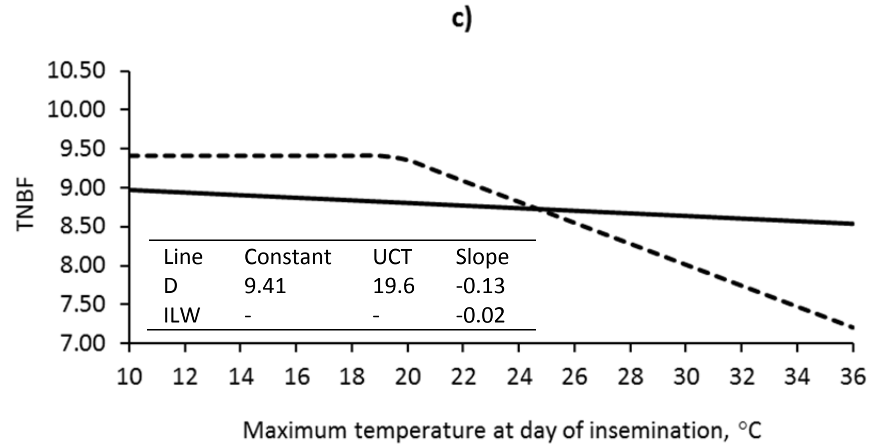
The goodness-of-fit tests for a linear effect of temperature on reproduction versus a plateau-linear effect of temperature on reproduction showed that for FR, LS, and TNBF of the D-line the plateau-linear model fitted significantly ($P < 0.05$) better than the linear model (Table 2.2). This implies that there is an UCT for the reproductive performance of the D-line. The UCT of this zone varied from 19.2°C for FR, to 21.7°C for LS, to 19.6°C for TNBF. Above these temperatures the estimated decrease in FR was 0.01 per °C, 0.05 per °C in LS, and 0.13 per °C in TNBF (Figure 2.4).

a)


0.90
0.85
0.80
0.75
0.70
0.65
FR
Line Constant UCT Slope
D 0.84 19.2 -0.01
ILW - - -
10 12 14 16 18 20 22 24 26 28 30 32 34 36
Maximum temperature at day of insemination, °C

b)


12.00
11.50
11.00
10.50
10.00
9.50
LS
Line Constant UCT Slope
D 11.15 21.7 -0.05
ILW - - -0.01
10 12 14 16 18 20 22 24 26 28 30 32 34 36
Maximum temperature at day of insemination, °C



Line	Constant	UCT	Slope
D	9.41	19.6	-0.13
ILW	-	-	-0.02

Figure 2.4 Estimated effect of maximum outside temperature at day of insemination on three reproductive performance traits (a = farrowing rate (FR), b = litter size (LS), c = total number piglets born per first insemination (TNBF)) for two sow lines, a Dutch purebred Yorkshire line (- - -) and an International purebred Large White line (—). For the Dutch line and the International line, significant estimates are given of the constant level of the reproductive performance trait where reproduction is not influenced by temperature (constant), of the upper critical temperature in °C (UCT), and of the slope of the decrease above the UCT (slope). All estimates were significant different from 0.

A significant effect of temperature was found on LS and TNBF of the ILW-line. To test if there was a linear or a plateau-linear relationship between LS and temperature, and between TNBF and temperature, a goodness-of-fit test was performed. For LS and TNBF of the ILW-line the linear regression model fitted significantly better than the plateau-linear model (Table 2.2). This implies that when temperature increases, LS and TNBF of the ILW-line decreases. However, the slope of this decrease was small. The estimated decrease in LS was 0.01 per °C, and 0.02 per °C in TNBF (Figure 2.4). Consequently, sows of the ILW-line have a higher reproductive performance for outside temperatures above 25°C than sows of the D-line.

2.4 Discussion

General

The results in this study indicate some clear differences in heat stress tolerance between two sow lines as measured by the differences seen in their reproductive performance. Negative influences of high temperature on reproductive performance of sows have been described by several authors (Wetteman et al., 1988; Tummaruk et al., 2004; Suriyasomboon et al., 2006), but none of them studied differences between sow lines. The line differences found in our study are an indication for genetic variation in heat stress tolerance between animals, which gives possibilities for selection on heat stress tolerance. In cattle and sheep, genetic variation in heat stress tolerance has been found (Ravagnolo et al., 2000; Finocchiarro et al., 2005).

Animals are considered to suffer from heat stress when temperature exceeds the UCT of the thermo-neutral zone (Black et al., 1993). Above the UCT of this zone the animal will reduce both production and reproduction to control body temperature (Bianca, 1976). In our study UCT was defined as the temperature above which reproductive performance starts to decrease. For the reproductive performance of sows of the D-line a clear UCT could be estimated. The UCT of D-line sows lies around 20°C. This is numerically less but in line with the UCT of 22°C reported by Black et al. (1993). For ILW-line sows no UCT for reproductive performance could be estimated. A significant adverse effect of temperature on LS and TNBF of ILW-line sows was found (0.01 per °C for LS, 0.02 per °C for TNBF). However, the decrease in reproductive performance of ILW-line sows with increasing outside temperature was less than in D-line sows.

Temperature effects on reproductive performance

It is well known that elevated temperature is a major factor responsible for reduced reproductive performance in livestock during hot seasons in tropical areas (e.g., Prunier et al., 1997; Peltoniemi et al., 1999; Ravagnolo and Misztal, 2002). Heat stress decreases expression of estrous behavior, alters ovarian follicular development, compromises oocytes competence, and inhibits embryonic development (Hansen et al., 2001). Wetteman et al. (1988) found that reduced reproductive performance due to heat stress during day 8 to 16 after mating is related to an altered maternal recognition of pregnancy.

When sows are exposed to high temperatures, the sow responds with elevated blood plasma concentrations of cortisol (Einarsson et al., 1996). Tsuma et al. (1995) showed that sows that failed to return to estrous after weaning had greater cortisol levels during lactation and after weaning and had decreased LH secretion after weaning than sows that returned to estrous directly after weaning. High temperatures during lactation have been found to decrease feed intake (Prunier et al., 1997). Reduced feed intake seems to restrict LH-release during lactation, which results in restricted follicle growth during lactation and affects follicle development after lactation. Impaired follicle development results in a smaller ovulation rate and an impaired quality of oocytes and follicular fluid, which may explain increased embryonic mortality. This can result in decreased LS at farrowing (Kemp et al., 2006). In an in-vitro study it was shown that exposure of porcine oocytes to high temperatures had a dramatic effect on the quality and the meiotic competence of oocytes (Barati et al., 2008).

Meteorological data

Temperature information at day of insemination originated from weather stations throughout Spain. These stations routinely collect daily information on temperature (Klein Tank et al., 2002). On-farm measurements could have reflected the weather conditions on the farm more accurately. However, for genetic evaluation large datasets are required and therefore, temperature data needs to be recorded on every farm. This information is not directly available. As a substitute for on-farm temperature measurements, records from nearby weather stations could be used. Freitas et al. (2006) concluded that records from nearby weather stations and records from weather stations further away from the farm provide satisfactory information for genetic evaluation of heat stress.

Heat stress refers to those meteorological elements that interfere with heat loss from the animal to the environment (Bianca, 1976). The meteorological element considered in our study was maximum temperature at day of insemination, and a significant adverse effect of high temperatures on reproductive performance was found. Other meteorological elements, such as relative humidity, average temperature, and minimum temperature, were ignored. However, in a study by Suriyasomboon et al. (2006), it was shown that not only elevated temperature, but also elevated humidity, had a negative impact on reproductive performance. Therefore, a worthwhile future study would be to investigate the combined effects of temperature and humidity on reproductive performance.

In our study heat stress was modeled linearly and plateau-linearly, and the cumulative effect of heat stress before and after day of insemination was ignored. However, high temperatures at day of insemination were found to be strongly correlated with temperatures in the period 4 weeks before and 4 weeks after mating (data not shown). Future studies should test which meteorological element has the largest effect on reproductive performance and should concern models in which the dynamics of heat stress can also be analyzed (e.g., cumulative effect of high temperatures).

Implications for pig breeding

Genetic potential of pigs has changed considerably in the past 50 years, and resulted in increased pig productivity (Brown-Brandl et al., 2004). In pig breeding, selection takes place on the nucleus level in mainly temperate climates and under improved environmental conditions throughout the year (Knap, 2005). In general, selection on production under these improved conditions has been shown to lead to an increased environmental sensitivity (Van der Waaij, 2004). Analogously here, sows of the D-line were selected on reproductive performance based on data collected in a temperate climate (The Netherlands), and these sows showed considerable reduction in reproductive performance with increasing temperatures in Spain. Selection on reproductive performance in the ILW-line was based on international data from mainly tropical countries (Brazil, Spain, Italy, Philippines), and these sows showed fewer problems with high temperatures. Therefore, even though D-line sows have a higher reproductive performance under temperate conditions than ILW-line sows, sows of the ILW-line are superior to sows of the D-line when outside temperatures exceed 25°C. This is a clear indication of a genotype × environment interaction. Our interpretation of these differences between D-line and ILW-line sows is that for the ILW-line families were selected, which did well for reproductive performance in these tropical countries, adapting therefore to the local environments.

At temperatures above the thermo-neutral zone gene networks within and across cells respond with a so-called cellular heat stress response. The heat shock transcription factor has been found to be the first responder for activation of this heat stress response (Sonna et al., 2002). This transcription factor coordinates the cellular response to thermal stress and affects expression of a wide variety of genes during heat stress. This expression has been associated with the regulation and the synthesis of heat shock proteins at the cellular level, which protect cells from damage (see review Collier et al., 2008). The variation in heat stress tolerance between animals and the role that heat shock transcription factor plays in response to heat stress suggests that there is an opportunity to improve heat stress tolerance via genetic selection.

In conclusion, the results from this study imply that there are important differences in the relationship between temperature and reproductive performance traits in two genetically different sow lines, and these differences suggest that genetic selection on sow heat stress tolerance may be possible.

2.5 Acknowledgements

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3

Heat stress effects on farrowing rate in sows: Genetic parameter estimation using within-line and crossbred models

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Abstract

The pork supply chain values steady and undisturbed piglet production. Fertilization and maintaining gestation in warm and hot climates is a challenge that can be potentially improved by selection. The objective of this study was to estimate 1) genetic variation for farrowing rate of sows in two dam lines and their reciprocal crosses; 2) genetic variation for farrowing rate's heat tolerance, which can be defined as the random regression slope of farrowing rate against increasing temperature at day of insemination, and the genetic correlation between farrowing rate and heat tolerance; 3) genetic correlation between farrowing rate in purebreds and crossbreds; and 4) genetic correlation between heat tolerance in purebreds and crossbreds. The estimates were based on 93,969 first insemination records per cycle from 24,456 sows inseminated between January 2003 and July 2008. These sows originated from a Dutch purebred Yorkshire dam line (D), an International purebred Large White dam line (ILW), and from their reciprocal crosses (RC) raised in Spain and Portugal. Within-line and crossbred models were used for variance component estimation. Heritability estimates for farrowing rate were 0.06, 0.07, and 0.02 using within-line models for D, ILW, and RC, respectively, and 0.07, 0.07, and 0.10 using the crossbred model, respectively. For farrowing rate, purebred-crossbred genetic correlations were 0.57 between D and RC and 0.50 between ILW and RC. When including heat tolerance in the within-line model, heritability estimates for farrowing rate were 0.05, 0.08, and 0.03 for D, ILW, and RC, respectively. Heritability for heat tolerance at 29.2°C was 0.04, 0.02, and 0.05 for D, ILW, and RC, respectively. Genetic correlations between farrowing rate and heat tolerance were close to 0 in all three lines. This study shows that genetic selection for farrowing rate and heat tolerance is possible. However, when this selection is based solely on purebred information, the expected genetic progress on farrowing rate and heat tolerance in crossbreds (commercial animals) would be inconsequential.

Key words: crossbreds, farrowing rate, genotype × environment interaction, heat tolerance, purebred-crossbred correlation, sows.

3.1 Introduction

Breeding organizations provide pigs to farms located around the world in environments which differ in altitude, temperature, feed quality, health status, and management. This requires pigs that can produce within a multitude of differing environments. High ambient temperature limits pig reproduction and is of increasing importance because of climate change and increased pig production in warm climates (FAO, 2006).

Reproductive performance is important for pig breeding programs; however, its genetic variation is low (Rydhmer, 2000). Farrowing rate can be defined as becoming pregnant from first insemination and subsequently maintaining pregnancy until farrowing. Farrowing rate of two dam lines responded differently to increasing temperatures, indicating that selection for heat tolerance might be possible (Bloemhof et al., 2008). Heat tolerance can be defined as the regression slope of farrowing rate against a heat load index (Ravagnolo and Misztal, 2000).

Commercial production pigs are crossbreds farmed all over the world. In contrast, selection is practiced mainly in temperate climates in nucleus herds using purebred pigs. Even if there would be genetic variation to improve farrowing rate and heat tolerance, the success of selection depends on how much genetic progress is realized in crossbred pigs. The genetic correlation between purebreds and crossbreds is a measure of efficiency of genetic selection in purebred animals on crossbred performance.

To assess genetic potential for breeding for farrowing rate and heat tolerance, we estimated 1) genetic variation for farrowing rate in two dam lines and their reciprocal crosses; 2) genetic variation for heat tolerance and the genetic correlation between farrowing rate and heat tolerance; 3) genetic correlation between farrowing rate in purebreds and crossbreds; and 4) genetic correlation between heat tolerance in purebreds and crossbreds.

3.2 Material and methods

Animal Care and Use Committee approval was not needed for this study because the data collected regularly for the TOPIGS breeding program (Vught, The Netherlands) were used. The TOPIGS breeding program operates according to the EFABAR code of conduct (Neeteson et al., 2006).

Table 3.1 Distribution of records for two dam lines and their reciprocal crosses.

	Dam line		Crossbreds	Overall dataset
	Dutch(D) (D*D)	International(ILW) (ILW*ILW)	(D*ILW)/ (ILW*D)	
# farms	17	16	20	33
# sows	6,565	13,835	4,056	24,456
# observations	24,546	59,369	10,054	93,969

Data

Data consisted of 93,969 first insemination records, per cycle, from 24,456 sows inseminated between January 2003 and July 2008. Sows were housed on 20 farms in Spain and on 13 farms in Portugal. Sows originated from a Dutch purebred Yorkshire dam line (**D**), an International purebred Large White dam line (**ILW**), and from their reciprocal crosses (**RC**). Both purebred dam lines are part of the TOPIGS breeding program (Vught, The Netherlands).

Out of the total of 33 farms, 17 farms had only D-line sows and the other 16 farms had only ILW-line sows. The two purebred dam lines were never located on the same farm. The RC-line sows were housed together with either D-line or ILW-line sows on 20 out of these33 farms. The number of records in these farms is given in Table 3.1.

Sows ranged in parity from 1 to 14. For each first insemination record per parity the following information was available: sow identification number, line, date of birth, farm, parity, date of first insemination in that specific cycle, service sire, and farrowing rate. Farrowing rate was defined as a binary trait: 1 if the first insemination resulted in a pregnancy and gestation length was longer than 108 days, or if piglets born from first insemination was at least 1. Otherwise farrowing rate was considered as 0. For sows culled after first insemination with culling reason reproductive failure farrowing rate was 0. Other sows culled after first insemination were removed from the dataset.

Meteorological data were obtained from the European Climate Assessment Dataset and included daily maximum outside temperature for 8 Spanish and 3 Portuguese weather stations (Klein Tank et al., 2002). Each insemination record in our dataset was assigned the daily maximum temperature from the nearest weather station on day of insemination. Average distance between farm and weather station was 117 kilometers (range in distance: 25-237 kilometers). These data should fairly represent the temperature at these farms. Freitas et al. (2006) estimated a correlation of 0.9 between on-farm temperature data and weather station temperature in the USA, even for weather stations more than 300 kilometers away from the farm.

Definition of heat tolerance

A previous study (Bloemhof et al., 2008) showed that farrowing rate of a sow remains fairly steady over a range of low and medium temperatures but starts decreasing above the upper critical temperature (**UCT**). However, the decrease in farrowing rate may be different between sows. The UCT above which farrowing rate is linearly affected has been estimated to be 19.2°C (Bloemhof et al., 2008). According to this, the heat load index was defined as the deviation of the maximum temperature on the day of insemination from 19.2°C, when maximum temperature on the day of insemination was higher than 19.2°C. Otherwise the heat load index was set to 0. Almost 46% of the observations had a heat load index of 0, and 54% of the observations had a heat load index which was larger than 0. For example, if the temperature on a day of insemination was 29.2°C then the heat load index was 10. Heat tolerance was then defined as relative change in farrowing rate per unit change in heat load index. It was estimated through the slope of a random regression line considering farrowing rate as the dependent variable (y-axis) and the heat load index as the independent variable (x-axis).

Within line analysis

To estimate (co)variance components for farrowing rate within each of three lines D, ILW, and RC, the following repeatability model was used:

$$y = Xb + Za + Wc + Fm + Us + e \qquad [1]$$

where *y* is a vector of liabilities to farrowing rate, *b* is a vector of the fixed effect of parity, *a* is a vector of the random genetic animal effect, *c* is a vector of the random permanent non-genetic animal effect, *m* is a vector of the random farm-year-month of insemination effect of the sow, *s* is a vector of the random service sire effect, *e* is a vector of the random residual effect, and *X*, *Z*, *W*, *F*, and *U* are the respective incidence matrices.

Variances were:

$$Var\begin{bmatrix} a_{fr} \\ pe_{fr} \\ fym \\ ss \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma^2_{a_{fr}} & 0 & 0 & 0 & 0 \\ 0 & \mathbf{I}_{pe}\sigma^2_{pe_{fr}} & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}_{fym}\sigma^2_{fym} & 0 & 0 \\ 0 & 0 & 0 & \mathbf{I}_{ss}\sigma^2_{ss} & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}_e\sigma^2_e \end{bmatrix}$$

where **A** is the additive relationship matrix, $\mathbf{I}_{pe}$, $\mathbf{I}_{fym}$,$\mathbf{I}_{ss}$, $\mathbf{I}_e$ are identity matrices and $\sigma^2_{a_{fr}}, \sigma^2_{pe_{fr}}, \sigma^2_{fym}, \sigma^2_{ss}, \sigma^2_e$ are animal, permanent environmental, farm-year-month, service sire, and residual variances, respectively.

To estimate (co)variance components simultaneously for farrowing rate and heat tolerance within each of three lines D, ILW, and RC, the following repeatability model was used:

$$y = Xb + Za_{fr} + Ha_{ht} + Wc_{fr} + Pc_{ht} + Fm + Us + e \qquad [2]$$

where a_{fr} is a vector of random genetic animal effects for overall farrowing rate; a_{ht} is a vector of random genetic animal effects for tolerance slopes (farrowing rate against the heat load index); c_{fr} is a vector of random permanent non genetic animal effects for overall farrowing rate level; c_{ht} is a vector of random permanent non genetic animal effects for tolerance slopes, and *Z*, *H*, *W*, and *P* are the respective incidence matrices. Other terms are as explained for model [1].

Variances were:

$$Var\begin{bmatrix} a_{fr} \\ a_{ht} \\ pe_{fr} \\ pe_{ht} \\ fym \\ ss \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma^2_{a_{fr}} & \mathbf{A}\sigma_{a_{fr}a_{ht}} & 0 & 0 & 0 & 0 & 0 \\ \mathbf{A}\sigma_{a_{fr}a_{ht}} & \mathbf{A}\sigma^2_{a_{ht}} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}_{pe}\sigma^2_{pe_{fr}} & \mathbf{I}_{pe}\sigma_{pe_{fr}pe_{ht}} & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}_{pe}\sigma_{pe_{fr}pe_{ht}} & \mathbf{I}_{pe}\sigma^2_{pe_{ht}} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}_{fym}\sigma^2_{fym} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{I}_{ss}\sigma^2_{ss} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{I}_e\sigma^2_e \end{bmatrix}$$

Compared to model 1 the new variances here are $\sigma^2_{a_{ht}}$ and $\sigma^2_{pe_{ht}}$ which are the genetic heat tolerance variance and the permanent environmental heat tolerance variance, respectively. The covariances $\sigma_{a_{fr}a_{ht}}$ and $\sigma_{pe_{fr}pe_{ht}}$ represent the covariance between the genetic farrowing rate effect and the genetic heat tolerance effect and the covariance between the permanent environmental farrowing rate effect and the permanent environmental heat tolerance effect.
Variances resulting from model 2 were used to calculate heritabilities for farrowing rate as:

$$\frac{\sigma^2_{a_{fr}}}{\sigma^2_{a_{fr}} + \sigma^2_{pe_{fr}} + \sigma^2_{fym} + \sigma^2_{ss} + \sigma^2_{e}}$$

Heritability for heat tolerance at heat load index *x* was calculated as follows according to Ravagnolo and Misztal (2000):

$$\frac{x^2\sigma^2_{a_{ht}}}{\sigma^2_{a_{fr}} + (x^2\sigma^2_{a_{ht}}) + \sigma^2_{pe_{fr}} + (x^2\sigma^2_{pe_{ht}}) + \sigma^2_{fym} + \sigma^2_{ss} + \sigma^2_{e}}$$

Crossbred model analysis

In this analysis, the (co)variance components for farrowing rate were estimated considering farrowing rate in lines D, ILW, and RC as three different traits and the genetic correlations between purebreds (D and ILW) and their crossbred (RC) offspring were estimated. The crossbred model proposed by Lo et al. (1997) was considered; however, no separate dominance effect was included. A multi-trait repeatability model was used:

$$\begin{bmatrix} y_D \\ y_I \\ y_C \end{bmatrix} = \begin{bmatrix} X_D & 0 & 0 \\ 0 & X_I & 0 \\ 0 & 0 & X_C \end{bmatrix} \begin{bmatrix} b_D \\ b_I \\ b_C \end{bmatrix} + \begin{bmatrix} Z_D & 0 & 0 & 0 \\ 0 & 0 & Z_I & 0 \\ 0 & Z_{DC} & 0 & Z_{IC} \end{bmatrix} \begin{bmatrix} a_D \\ a_{DC} \\ a_I \\ a_{IC} \end{bmatrix} +$$

$$\begin{bmatrix} W_D & 0 & 0 \\ 0 & W_I & 0 \\ 0 & 0 & W_C \end{bmatrix} \begin{bmatrix} c_D \\ c_I \\ c_C \end{bmatrix} + \begin{bmatrix} F_D & 0 & 0 \\ 0 & F_I & 0 \\ 0 & 0 & F_C \end{bmatrix} \begin{bmatrix} m_D \\ m_I \\ m_C \end{bmatrix} + \qquad [3]$$

$$\begin{bmatrix} U_D & 0 & 0 \\ 0 & U_I & 0 \\ 0 & 0 & U_C \end{bmatrix} \begin{bmatrix} s_D \\ s_I \\ s_C \end{bmatrix} + \begin{bmatrix} e_D \\ e_I \\ e_C \end{bmatrix}$$

where subscript *D* represents line D, subscript *I* represents line ILW, and subscript *C* represents the crossbreds; *y* is a vector of liabilities to farrowing rate; *b* is a vector of the fixed effect of parity; a_D and a_I, are vectors of the random additive genetic animal effects; a_{DC} is a vector of the random genetic effect for the D-line parent of crossbred RC; a_{IC} is a vector of the random genetic effect for the ILW-line parent of crossbred RC; *c* is a vector of the random permanent non-genetic animal effect, *m* is a vector of the random farm-year-month of insemination effect of the sow, *s* is a vector of the random service sire effect, *e* is a vector of the random residual effect, and *X*, *Z*, *W*, *F*, and *U* are the respective incidence matrices.

The additive genetic effect of crossbreds in the model was partitioned as the effect of the parents and was calculated as $a_{fr\,C} = a_{fr\,DC} + a_{fr\,IC} + \Phi_{fr\,C}$, where $\Phi_{fr\,C}$ is the Mendelian sampling which in the model is included in the random permanent non-genetic animal effect. It was assumed that

$$\sigma^2_{a\,fr_{DC}} = \tfrac{1}{4}\sigma^2_{a\,fr_C}, \sigma^2_{a\,fr_{IC}} = \tfrac{1}{4}\sigma^2_{a\,fr_C}, \sigma^2_{\Phi fr} = \tfrac{1}{2}\sigma^2_{a\,fr_C} .$$

Heritabilities for crossbreds were calculated as

$$(2*(\sigma^2_{a\,fr_{DC}} + \sigma^2_{a\,fr_{IC}}))(\sigma^2_{a\,fr_{DC}} + \sigma^2_{a\,fr_{IC}} + \sigma^2_{pe\,fr} + \sigma^2_{fym} + \sigma^2_{ss} + \sigma^2_{e})^{-1} ,$$

where $\sigma^2_{a\,fr_{DC}}$ and $\sigma^2_{a\,fr_{IC}}$ are the additive genetic variances for the parent of crossbred RC descending from lines D and ILW, respectively.

Variances of random effects other than the genetic effect were assumed to be uncorrelated between the three lines and therefore similar to those for model 1. The variances of the genetic effect were assumed to be:

$$Var\begin{bmatrix} a_{fr_D} \\ a_{fr_{DC}} \\ a_{fr_I} \\ a_{fr_{IC}} \end{bmatrix} = \begin{bmatrix} \sigma^2_{a\,fr_D} & \sigma_{a\,fr_D a\,fr_{DC}} & 0 & 0 \\ \sigma_{a\,fr_D a\,fr_{DC}} & \sigma^2_{a\,fr_{DC}} & 0 & 0 \\ 0 & 0 & \sigma^2_{a\,fr_I} & \sigma_{a\,fr_I a\,fr_{IC}} \\ 0 & 0 & \sigma_{a\,fr_I a\,fr_{IC}} & \sigma^2_{a\,fr_{IC}} \end{bmatrix} \otimes \mathbf{A}$$

To estimate (co)variance components simultaneously for farrowing rate and heat tolerance using purebred and crossbred data, farrowing rate and heat load recorded on lines D, ILW, and RC were considered as three different traits, with a genetic correlation between purebreds and their crossbred offspring:

$$\begin{bmatrix} y_D \\ y_I \\ y_C \end{bmatrix} = \begin{bmatrix} X_D & 0 & 0 \\ 0 & X_I & 0 \\ 0 & 0 & X_C \end{bmatrix} \begin{bmatrix} b_D \\ b_I \\ b_C \end{bmatrix} + \begin{bmatrix} Z_D & 0 & 0 & 0 \\ 0 & 0 & Z_I & 0 \\ 0 & Z_{DC} & 0 & Z_{IC} \end{bmatrix} \begin{bmatrix} a_{fr\,D} \\ a_{fr\,DC} \\ a_{fr\,I} \\ a_{fr\,IC} \end{bmatrix} +$$

$$\begin{bmatrix} H_D & 0 & 0 & 0 \\ 0 & 0 & H_I & 0 \\ 0 & H_{DC} & 0 & H_{IC} \end{bmatrix} \begin{bmatrix} a_{ht\,D} \\ a_{ht\,DC} \\ a_{ht\,I} \\ a_{ht\,IC} \end{bmatrix} +$$

$$\begin{bmatrix} W_D & 0 & 0 \\ 0 & W_I & 0 \\ 0 & 0 & W_C \end{bmatrix} \begin{bmatrix} c_{fr\,D} \\ c_{fr\,I} \\ c_{fr\,C} \end{bmatrix} + \begin{bmatrix} P_D & 0 & 0 \\ 0 & P_I & 0 \\ 0 & 0 & P_C \end{bmatrix} \begin{bmatrix} c_{ht\,D} \\ c_{ht\,I} \\ c_{ht\,C} \end{bmatrix} +$$

$$\begin{bmatrix} F_D & 0 & 0 \\ 0 & F_I & 0 \\ 0 & 0 & F_C \end{bmatrix} \begin{bmatrix} m_D \\ m_I \\ m_C \end{bmatrix} + \begin{bmatrix} U_D & 0 & 0 \\ 0 & U_I & 0 \\ 0 & 0 & U_C \end{bmatrix} \begin{bmatrix} s_D \\ s_I \\ s_C \end{bmatrix} + \begin{bmatrix} e_D \\ e_I \\ e_C \end{bmatrix} \qquad [4]$$

where $a_{fr\,D}$ and $a_{fr\,I}$ are vectors of random additive genetic animal effects for overall farrowing rate level; $a_{fr\,DC}$ is a vector of the random additive genetic effect for overall farrowing rate level for the D-line parent of crossbred RC; $a_{fr\,IC}$ is a vector of the random additive genetic effect for overall farrowing rate level for the ILW-line parent of crossbred RC; $a_{ht\,D}$ and $a_{ht\,I}$ are vectors of random additive genetic animal effects for tolerance slopes (farrowing rate against the heat load index); $a_{ht\,DC}$ is a vector of the random additive genetic effect for tolerance slopes (farrowing rate against the heat load index) for the D-line parent of crossbred RC; $a_{ht\,IC}$ is a vector of the random additive genetic effect for tolerance slopes (farrowing rate against the heat load index) for the ILW-line parent of crossbred RC; c_{fr} is a vector of random permanent non-genetic animal effects for overall farrowing rate level; c_{ht} is a vector of random permanent non-genetic animal effects for tolerance slopes, and Z, H, W, and P are the respective incidence matrices. Other terms are as explained for model [3].

Variance structure was assumed to be the same as those of model 2, except for the genetic farrowing rate variance and the genetic heat tolerance variance which are presented in Figure 3.1.

$$Var\begin{bmatrix} a_{fr_D} \\ a_{fr_{DC}} \\ a_{ht_D} \\ a_{ht_{DC}} \\ a_{fr_I} \\ a_{fr_{IC}} \\ a_{ht_I} \\ a_{ht_{IC}} \end{bmatrix} = \begin{bmatrix} \sigma^2_{a\,fr_D} & \sigma_{a\,fr_D a\,fr_{DC}} & \sigma_{a\,fr_D\,a\,ht_D} & \sigma_{a\,fr_D\,a\,ht_{DC}} & 0 & 0 & 0 & 0 \\ \sigma_{a\,fr_D a\,fr_{DC}} & \sigma^2_{a\,fr_{DC}} & \sigma_{a\,fr_{DC}\,a\,ht_D} & \sigma_{a\,fr_{DC}\,a\,ht_{DC}} & 0 & 0 & 0 & 0 \\ \sigma_{a\,fr_D\,a\,ht_D} & \sigma_{a\,fr_{DC}\,a\,ht_D} & \sigma^2_{a\,ht_D} & \sigma_{a\,ht_D\,a\,ht_{DC}} & 0 & 0 & 0 & 0 \\ \sigma_{a\,fr_D\,a\,ht_{DC}} & \sigma_{a\,fr_{DC}\,a\,ht_{DC}} & \sigma_{a\,ht_D\,a\,ht_{DC}} & \sigma^2_{a\,ht_{DC}} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \sigma^2_{a\,fr_I} & \sigma_{a\,fr_I a\,fr_{IC}} & \sigma_{a\,fr_I\,a\,ht_I} & \sigma_{a\,fr_I\,a\,ht_{IC}} \\ 0 & 0 & 0 & 0 & \sigma_{a\,fr_I a\,fr_{IC}} & \sigma^2_{a\,fr_{IC}} & \sigma_{a\,fr_{IC}\,a\,ht_I} & \sigma_{a\,fr_{IC}\,a\,ht_{IC}} \\ 0 & 0 & 0 & 0 & \sigma_{a\,fr_I\,a\,ht_I} & \sigma_{a\,fr_{IC}\,a\,ht_I} & \sigma^2_{a\,ht_I} & \sigma_{a\,ht_I\,a\,ht_{IC}} \\ 0 & 0 & 0 & 0 & \sigma_{a\,fr_I\,a\,ht_{IC}} & \sigma_{a\,fr_{IC}\,a\,ht_{IC}} & \sigma_{a\,ht_I\,a\,ht_{IC}} & \sigma^2_{a\,ht_{IC}} \end{bmatrix} \otimes \mathbf{A}$$

Figure 3.1 Variance structure model 4.

Computations

Variance components were estimated using a Bayesian threshold model via Gibbs sampling (THRGIBBS1F90-software; Tsuruta and Misztal, 2006). The THRGIBBS1F90 program is based on a probit model in MCMC setting (Sorensen and Ganiola, 2002). Every 10th sample was saved to calculate posterior means and SE of variance components, heritabilities and correlations. Convergence was visualized by plotting of Gibbs samples.The first 25,000 to 375,000 samples were removed as burn-in, and a total of 125,000 to 375,000 samples were used for the final computations.

3.3 Results

Line differences in traits

Average farrowing rate was 83% across all lines. Crossbred sows had the greatest farrowing rate (86%), and D-line sows had the smallest farrowing rate (82%). The ILW-line sows had the highest heat load index on day of insemination (5.0), and crossbred sows had the lowest heat load index on day of insemination (3.8); however, these differences were not significant (Table 3.2).

Within line analysis: Farrowing rate

Heritability estimates for farrowing rate were lowest for crossbred sows (0.02 ± 0.01) and highest for ILW-line sows (0.07 ± 0.01; Table 3.3). Genetic variances for farrowing rate were equal for D- and ILW-line sows (0.08 ± 0.02); however, farrowing rate genetic variance of crossbred sows was only a quarter of those of the purebred sows (0.02 ± 0.02; Table 3.3). Permanent environmental variance was one-half of the farrowing rate genetic variance in D- and ILW-line sows (0.04 ± 0.02). In crossbred sows permanent environmental variance was 3 times larger (0.06 ± 0.03) than the farrowing rate genetic variance (0.02 ± 0.02). Farm-year-month, service sire and residual variances did not differ much between lines. Smallest SE of estimates were found in ILW-line sows, which had the largest number of observations.

Within line analysis: Farrowing rate including heat tolerance

Similar to the model excluding heat tolerance, heritability estimates for farrowing rate were least for crossbred sows (0.03 ± 0.02) and highest for ILW-line sows (0.08 ± 0.01; Table 3.4). Heritability estimates for heat tolerance were lowest for ILW-line sows (0.02 ± 0.01) and highest for crossbred sows (0.05 ± 0.03; Table 3.4). Including heat tolerance in the model did not change heritability estimates for farrowing rate when comparing Table 3.3 and Table 3.4.

Table 3.2 Mean and SD (in parenthesis) of farrowing rate and heat load index of two dam lines and their reciprocal crosses.

	Dam line		Crossbreds	Overall dataset
	Dutch(D) (D*D)	International(ILW) (ILW*ILW)	(D*ILW)/ (ILW*D)	
Farrowing rate	0.82 (0.39)	0.83 (0.38)	0.86 (0.35)	0.83 (0.38)
Heat load index	4.0 (5.2)	5.0 (6.0)	3.8 (5.1)	4.6 (5.7)

Table 3.3 Estimated heritabilities, variance components, and corresponding SE (in parenthesis) for farrowing rate (*fr*) using within-line analysis for two dam lines and their reciprocal crosses.

Parameter	Description	Dam line		Crossbreds
		Dutch (D) (D*D)	International(ILW) (ILW*ILW)	(D*ILW)/ (ILW*D)
h^2_{fr}	heritability for farrowing rate	0.06(0.01)	0.07(0.01)	0.02(0.01)
$\sigma^2_{a_{fr}}$	genetic variance for *fr*	0.08(0.02)	0.08(0.01)	0.02(0.02)
$\sigma^2_{pe_{fr}}$	permanent environmental variance for *fr*	0.04(0.02)	0.04(0.01)	0.06(0.03)
σ^2_{fym}	farm year month of insemination variance	0.10(0.01)	0.08(0.01)	0.09(0.02)
σ^2_{ss}	service sire variance	0.02(0.01)	0.02(0.00)	0.02(0.01)
σ^2_{e}	residual variance	1.00(0.01)	1.00(0.01)	1.00(0.02)
σ^2_{p}	phenotypic variance	1.24(0.03)	1.22(0.02)	1.20(0.04)

Genetic variances for farrowing rate and for heat tolerance differed between lines (Table 3.4). Genetic variance for heat tolerance in crossbred sows (0.08 ± 0.05) at heat load index 10 was twice as large as the genetic variance (0.04 ± 0.03) for their farrowing rates. Genetic variance for heat tolerance in D-line sows (0.06 ± 0.02) at heat load index 10 was as large as the genetic variance for farrowing rate in D-line sows (0.06 ± 0.02). Genetic variance for heat tolerance in ILW-line sows at heat load index 10 was close to 0 (0.02 ± 0.01).

Genetic correlations between farrowing rate and heat tolerance were close to 0 in all the three lines with large standard errors of the estimates (Table 3.4).

Table 3.4 Estimated heritabilities, variance components, and genetic correlations, with corresponding SE (in parenthesis) for farrowing rate (*fr)* and heat tolerance (*ht*) using within-line analysis for two dam lines and their reciprocal crosses.

Parameter	Description	Dam line		Crossbreds
		Dutch(D) (D*D)	International(ILW) (ILW*ILW)	(D*ILW)/ (ILW*D)
h^2_{fr}	heritability for farrowing rate	0.05(0.02)	0.08(0.01)	0.03(0.02)
h^2_{ht}	heritability for heat tolerance[1]	0.04(0.01)	0.02(0.01)	0.05(0.03)
$rg_{fr,ht}$	genetic correlation between *fr* and *ht*	0.16(0.32)	-0.36(0.17)	-0.06(0.40)
$\sigma^2_{a_{fr}}$	genetic variance for *fr*	0.06(0.02)	0.10(0.01)	0.04(0.03)
$100\sigma^2_{a_{ht}}$	genetic variance for *ht*[1]	0.06(0.02)	0.02(0.01)	0.08(0.05)
$\sigma^2_{pe_{fr}}$	permanent environmental variance for *fr*	0.08(0.02)	0.03(0.01)	0.10(0.05)
$100\sigma^2_{pe_{ht}}$	permanent environmental variance for *ht*[1]	0.04(0.02)	0.01(0.01)	0.10(0.07)
σ^2_{fym}	farm year month of insemination variance	0.07(0.01)	0.08(0.01)	0.10(0.02)
σ^2_{ss}	service sire variance	0.03(0.01)	0.02(0.00)	0.02(0.01)
σ^2_{e}	residual variance	1.00(0.01)	1.00(0.01)	1.00(0.02)
σ^2_{p}	phenotypic variance	1.23(0.03)	1.23(0.02)	1.26(0.07)
$\sigma^2_{p_{ht}}$	total phenotypic variance for *ht*[1]	1.33(0.05)	1.26(0.02)	1.44(0.12)

[1] At heat load index 10 (= temperature of 29.2°C).

Table 3.5 Estimated heritabilities, variance components, and genetic correlations, with corresponding SE (in parenthesis) for farrowing rate (*fr*) using crossbred-model analysis for two dam lines and their reciprocal crosses.

Parameter	Description	Dam line Dutch (D) (D*D)	 International (ILW) (ILW*ILW)	Crossbreds (D*ILW)/ (ILW*D)
h^2_{fr}	heritability for farrowing rate	0.07(0.01)	0.07(0.01)	0.10(0.04)
rpc_{fr}	genetic correlation between *fr* in purebreds and its descending crossbred	0.57(0.57)	0.50(0.25)	
$\sigma^2_{a_{fr}}$	genetic variance for *fr*	0.09(0.02)	0.09(0.01)	0.13(0.06)
$\sigma^2_{pe_{fr}}$	permanent environmental variance for *fr*	0.02(0.01)	0.04(0.01)	0.09(0.03)
σ^2_{fym}	farm year month of insemination variance	0.12(0.01)	0.09(0.01)	0.09(0.02)
σ^2_{ss}	service sire variance	0.03(0.01)	0.02(0.01)	0.03(0.01)
σ^2_{e}	residual variance	1.00(0.01)	1.00(0.01)	1.00(0.01)
σ^2_{p}	phenotypic variance	1.27(0.03)	1.23(0.02)	1.28(0.05)

Crossbred model analysis: Farrowing rate

Heritability estimates for farrowing rate from crossbred-model analysis (Table 3.5) were highest for sows from the crossbred line (0.10 ± 0.04). The heritability estimates for D- and ILW-line sows were quite similar (0.07 ± 0.01). Farrowing rate genetic variances from crossbred-model analysis (Table 3.5) were largest for crossbred sows (0.13 ± 0.06). The D- and ILW-line sows had similar farrowing rate genetic variance estimates (0.09 ± 0.02). Permanent environmental variance was smallest in D-line sows (0.02 ± 0.01) and greatest in crossbred sows (0.09 ± 0.03). Farm-year-month, service sire, and residual variances were generally similar between lines.

Genetic correlations between purebreds and crossbreds were moderately positive ($r_{fr_D fr_{DC}}$: 0.57 ± 0.57; $r_{fr_I fr_{IC}}$: 0.50 ± 0.25), SE, however, were large.

Table 3.6 Estimated heritabilities, variance components, and genetic correlations with corresponding SE (in parenthesis) for farrowing rate (*fr*) and heat tolerance (*ht*) using crossbred-model analysis for 2 dam lines and their reciprocal crosses.

Parameter	Description	Dam line		Crossbreds (D*ILW)/ (ILW*D)
		Dutch (D) (D*D)	International(I) (ILW*ILW)	
h^2_{fr}	heritability for farrowing rate	0.05(0.01)	0.08(0.01)	0.19(0.07)
h^2_{ht}	heritability for heat tolerance[1]	0.04(0.01)	0.02(0.01)	0.36(0.08)
$rg_{fr,ht}$	genetic correlation between *fr* and *ht*	0.31(0.20)	-0.37(0.15)	-0.57(0.15)
rpc_{fr}	genetic correlation between *fr* in purebreds and its descending crossbred	0.62(0.32)	0.32(0.27)	
rpc_{ht}	genetic correlation between *ht* in purebreds and its descending crossbred	0.15(0.21)	-0.23(0.27)	
$\sigma^2_{a_{fr}}$	genetic variance for *fr*	0.06(0.02)	0.10(0.02)	0.29(0.12)
$100\sigma^2_{a_{ht}}$	genetic variance for *ht*[1]	0.06(0.02)	0.03(0.01)	0.74(0.21)
$\sigma^2_{pe_{fr}}$	permanent environmental variance for *fr*	0.09(0.02)	0.04(0.01)	0.18(0.06)
$100\sigma^2_{pe_{ht}}$	permanent environmental variance for *ht*[1]	0.09(0.02)	0.04(0.01)	0.36(0.12)
σ^2_{fym}	farm year month of insemination variance	0.09(0.01)	0.08(0.01)	0.11(0.01)
σ^2_{ss}	service sire variance	0.03(0.01)	0.02(0.01)	0.04(0.01)
σ^2_{e}	residual variance	1.00(0.01)	1.00(0.01)	1.00(0.01)
σ^2_{p}	phenotypic variance	1.27(0.03)	1.24(0.02)	1.46(0.10)
$\sigma^2_{p_{ht}}$	total phenotypic variance for *ht*[1]	1.43(0.05)	1.32(0.03)	2.05(0.19)

[1] at heat load index 10 (=equal to temperature of 29.2°C)

Crossbred model analysis: Farrowing rate including heat tolerance

Heritability estimate for farrowing rate from crossbred model analysis including heat tolerance (Table 3.6) was unexpectedly high for crossbred sows (0.19 ± 0.07). Heritability estimate for heat tolerance of crossbred sows was 0.36 ± 0.08 (Table 3.6), a value much greater than estimated using within-line analysis. Heritability estimates for farrowing rate and heat tolerance of D- and ILW-line sows (Table 3.6) were in line with the estimates using within-line analysis (Table 3.4). Estimates of mean variances for farrowing rate and heat tolerance using crossbred-model analysis for the three lines are shown in Table 3.6. Comparing these estimates with the estimates from within-line analysis (Table 3.4), variance estimates for D- and ILW-line sows were similar either using crossbred model or within-line analysis. Variance estimates for crossbred sows were extremely high (Table 3.6). Genetic variance for heat tolerance at a temperature of 29.2°C of crossbred sows was 25 times larger for crossbred sows compared with purebred sows. Also genetic variance for farrowing rate, permanent environmental variance for farrowing rate, and heat tolerance were much larger in crossbred sows than in purebred sows. However, SE of estimates were large too.

Genetic correlation between farrowing rate of D-line sows and its descending crossbreds was moderately positive (0.62 ± 0.32). Genetic correlation between farrowing rate of ILW-line sows and its descending crossbred was 0.32 ± 0.27. Genetic correlations between farrowing rate and heat tolerance were again close to 0 (Table 3.6), but SE were smaller than those from within-line analysis. Genetic correlations between heat tolerance of purebreds and heat tolerance of crossbreds were almost 0 ($r_{ht_D ht_{DC}}$: 0.15 ± 0.21; $r_{ht_I ht_{IC}}$: -0.23 ± 0.27) with SE than estimates.

3.4 Discussion

This study shows that both farrowing rate and heat tolerance are traits with low heritabilities, but traits that still exhibit genetic variance that could potentially be exploited by selection. Because genetic correlations between purebreds and descending crossbreds were all lower than unity for both farrowing rate and heat tolerance, inclusion of crossbred data in the evaluation of purebred animals is necessary to fully realize genetic improvement in commercial crossbred animals.

Farrowing rate

Heritability for farrowing rate in purebred sows estimated using within-line analysis was 0.07 ± 0.01. The few other studies on the maternal heritability of farrowing rate have found lower estimates, below 0.04 (Leukkunen, 1984; Hanenberg et al., 2001). These studies used linear models which are known to underestimate the true heritability of categorical traits compared with the threshold model used in the present study. For instance, the heritability estimate of Hanenberg et al. (2001) becomes 0.075 ± 0.005 when transformed to the underlying liability scale using the formula of Dempster and Lerner (1950). Holm et al. (2005) estimated a maternal heritability of 0.03 using a threshold model for a trait considering if a gilt or sow was inseminated again within 100 days after first insemination. Accordingly, a large part of variation in pregnancy success is due to environmental factors, such as AI-management, estrus monitoring, and season (Rydhmer, 2000; Hanenberg et al., 2001).

The heritability of farrowing rate observed here is very low compared to the heritability of pig production traits such as back-fat thickness, which has a heritability of around 45% (Clutter, 2011). However, the advantage of improving farrowing rate by breeding compared to improving farrowing rate by management is that breeding results in a permanent change in the genetic composition of the pig breeding population. Even for a trait such as litter size with a heritability of around 10%, substantial genetic improvement has been realized (Dekkers et al., 2011). Moreover, when low heritability traits are economically very important, even minor genetic changes have a big impact on the industry profit.

In the USA and the Netherlands, more than 10% of the sows do not farrow from first insemination and return to estrus (PigCHAMP, 2010b; Kengetallenspiegel., 2011). In Spain, the number of sows returning to estrus after first insemination is even greater, around 17% (PigCHAMP, 2010a). Farrowing rate directly affects number of litters per sow per year and therefore the number of non-productive sow days. Non-productive sow days are the days in which a sow is not lactating or gestating (Wilson et al., 1986). The cost of one non-productive sow day has been estimated to be €2.20 in the Netherlands (Wageningen Livestock Research, 2011), which includes costs of feed and loss in piglet production. For Spain and Portugal, no literature could be found on the costs of non-productive sow days but we expect it to be also around €2.20/day. Return to estrus is the main reason for culling of young sows (Engblom et al., 2007). This shows that improving farrowing rate by breeding can be highly profitable as the number of non-productive sow days can be reduced, litters per sow per year can be increased and unplanned sow removal can be prevented.

Heat tolerance

Genetic variation for heat tolerance exists, and therefore there are possibilities for genetic improvement in heat tolerance. The additive variance for heat tolerance at a heat load index of 10 was as large as the additive variance for farrowing rate for the sows from the D-line and twice as large as for the crossbred sows. These results are in line with previous studies in which additive variances for heat tolerance have been found to be important for non-return rate and milk production in dairy cattle, for milk yield in sheep, and for growth in finisher pigs. Under increased temperature, the additive variances for heat tolerance were as large as the additive variances for the production traits under non-stressed lower temperature (Ravagnolo and Misztal, 2000, 2002; Finocchiaro et al, 2005; Zumbach et al., 2008). Heritability estimates for heat tolerance of D-line and crossbred sows at a heat load index of 10 were low (0.05 ± 0.03 and 0.04 ± 0.01, respectively) and similar to the heritability estimates for farrowing rate. Sows from the ILW-line showed the smallest genetic variation for heat tolerance, with heritability estimate of 0.02 ± 0.01 at heat load index 10. This is in line with a previous study in which no effect of temperature was found on farrowing rate of ILW-line sows (Bloemhof et al., 2008). Selection on reproductive performance in ILW-line sows is based on international data mainly from tropical countries (Brazil, Spain, Italy, Philippines). This increases reproductive performance especially in warm climate, potentially leading to a flatter temperature reaction norm and thus indirect selection on heat tolerance. Although speculative, this may have resulted in the low genetic variance for heat tolerance estimated in this study.

Selection for production traits often increases environmental sensitivity (Van der Waaij, 2004). This was not supported by our results. Genetic correlations between farrowing rate and heat tolerance were all around 0. In finisher pigs, a genetic correlation of -0.5 between carcass weight and heat tolerance has been reported (Zumbach et al., 2008). In dairy cattle as well, genetic correlations between milk production and heat tolerance were negative, ranging from -0.30 to -0.95 (Ravagnolo and Misztal, 2000; Aguilar et al., 2009). These reports imply that current selection strategies for reproduction and production traits in moderate climates reduce heat tolerance. However, this was not supported by our results.

It is anticipated that heat tolerance may become even more important as a limiting factor for global pig production mainly because of three reasons. First, genetic progress in pigs in the past 50 years has led to more lean animals, resulting in an increase of internal heat production of pigs. Greater internal heat production reduces heat tolerance capacity, resulting in increased susceptibility to heat stress (Brown-Brandl et al., 2001). Second, temperature is expected to increase worldwide as a result of climate change (Hofmann, 2010). Finally, meat production is expected to double from 229 million tonnes (in 1999) to 465 million tonnes (in 2050), the growth predicted to be the fastest in warm climates such as Latin America and South and East Asia (FAO, 2006).

The present and our previous study (Bloemhof et al., 2008) imply that the linear-plateau model proposed by Ravagnolo and Misztal (2000) is applicable to evaluate sows for heat tolerance as well. Even though the linear-plateau model has its limitations, the model may be good enough to rank animals for heat tolerance. To ensure firm breeding value estimation for heat tolerance for all breeding candidates in a practical breeding programme, it should be ensured that selection candidates have relatives tested under both temperate and hot conditions in the field. Testing animals in experimental heat chambers might also be a powerful alternative, yet this is unpractical on routine basis.

Crossbreds and farrowing rate

Our results showed that pigs ranked the best as purebreds for farrowing rate are not always breeding the best crossbreds. Since the breeding goal is crossbred reproductive performance, genetic gain at crossbred level can be best improved using crossbred models. In these models, purebred animals are evaluated using data on both purebred and crossbred performance.

Heritability and variance component estimates for farrowing rate of purebreds obtained from the crossbred model analysis were similar to those from within-line analysis. In contrast, heritability estimates of crossbreds were increased when switching from within-line analysis to crossbred model analysis. Within-line analysis of crossbred animals assumes that their parents originate from one population. This assumption is obviously wrong since crossbred progeny descend from two different purebred lines. The crossbred model considers the two purebred lines separately and accounts therefore for gene frequency differences between purebreds which are caused by different selection strategies in both lines (Lutaaya et al., 2002).

Since the goal in pig breeding is to improve crossbred performance, such as growth and reproductive output, and selection is performed at purebred level, the importance of crossbred information increases with decreasing purebred-crossbred correlation. A purebred-crossbred correlation lower than 1 suggests dominance and gene frequency differences between purebred lines, and possible genotype × environment interactions when purebred and crossbred animals do not share the same environment (Wei and van der Werf, 1995; Lutaaya et al., 2002). A purebred-crossbred correlation below 0.8 would reduce the selection response at crossbred level when only purebred information is included in the selection scheme (Bijma and van Arendonk, 1998). In our study, genetic correlations between farrowing rate in purebreds and crossbreds were moderately positive ($r_{fr_D fr_{DC}}$: 0.57 ± 0.57; $r_{fr_I fr_{IC}}$: 0.50 ± 0.25). There are no previous estimates of this correlation because reproductive performance traits are not widely studied in purebred-crossbred systems.

In our study, purebred and crossbred sows were located on the same farms. Therefore, the r_{pc} estimated is the genetic correlation between purebreds and crossbreds that does not include potential genotype × environment interactions. In pig farming, purebred animals and crossbred animals are often not located on the same farm. Purebred animals are raised on nucleus farms with high management standards, such as increased biosecurity and more space per pig. Crossbred animals are raised on commercial farms with conventional health and increased pig density (Zumbach et al., 2007). Therefore it is possible that the r_{pc} for farrowing rate could be even less in the present study if purebred and crossbred animals would have been on different farms. Since the goal in pig breeding programs is to improve crossbred performance, such as growth and reproductive output, and the genetic correlation between purebreds and crossbreds estimated in our study was below 0.6, it is advisable to use a combined crossbred-purebred selection (CCPS) method to make sure genetic improvement is fully realized in commercial crossbred animals (Bijma and van Arendonk, 1998; Merks and Hanenberg, 1998).

Crossbreds and heat tolerance

To estimate purebred-crossbred correlations for heat tolerance, the crossbred model was adapted and a random regression term for heat tolerance was included. This resulted in a model in which 23 random components were fitted. Heritability and variance component estimates for farrowing rate and heat tolerance of purebreds obtained from the crossbred model analysis were similar to those from within-line analysis. Additive variance for farrowing rate of crossbreds from crossbred model analysis was 7 times larger than from within-line analysis. Additive heat tolerance variance of crossbreds from crossbred model analysis was 9 times larger than from within-line analysis. Plots of Gibbs samples (plots not shown) showed quite some instability, and it seemed that the crossbred parameters were not converged. Attempts to make the model simpler by removing permanent environmental heat tolerance effects or adjusting the model by including only sires of crossbred animals in the pedigree did not enhance convergence. In conclusion, we did not succeed in estimating purebred-crossbred correlations for heat tolerance. Estimating 23 random components in one analysis is quite ambitious and requires probably a larger dataset than used in our study or a dataset which is more balanced than ours.

Implications

Genetic selection for farrowing rate is possible, but if selection is solely based on purebred information, the expected genetic progress on farrowing rate in crossbreds (commercial animals) will be modest. The crossbred model allows evaluation of purebreds on the basis of purebred and crossbred performance simultaneously, revealing more genetic variance for crossbreds than the more simplistic within-line analysis. Adding heat tolerance to the within-line analysis increases genetic variance for farrowing rate even more. In D-line and crossbred sows that are sensitive to heat, additive variance for heat tolerance at a temperature of 29.2°C was as large as the additive variance for farrowing rate. Breeding for improved heat tolerance is therefore possible and may become important for pig breeding programs as a result of climate change and pig production moving to warm climates.

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4

Effect of daily environmental temperature on farrowing rate and total born in dam line sows

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Abstract

Heat stress is known to adversely affect reproductive performance of sows. However, it is important to know on which days or periods during the reproduction cycle heat stress has the greatest effects for designing appropriate genetic or management strategies. Therefore, this study was conducted to identify days and periods that have greatest effects on farrowing rate and total born of sows using five different measures of heat stress. The data consisted of 22,750 records on 5,024 Dutch Yorkshire dam line sows from 16 farms in Spain and Portugal. Heat stress on a given day was measured in terms of maximum temperature, diurnal temperature range and heat load. The heat load was estimated using three definitions considering different upper critical temperatures. Identification of days during the reproduction cycle that had maximum effect was based on the Pearson correlation between the heat stress variable and the reproduction trait, estimated for each day during the reproduction cycle. Polynomial functions were fitted to describe the trends of these correlations and the days with greatest negative correlation were considered as days with maximum effect. Correlations were greatest for maximum temperature, followed by those for heat load and diurnal temperature range. Correlations for both farrowing rate and total born were stronger in gilts than in sows. This implies that heat stress has a stronger effect on reproductive performance of gilts than of sows. Heat stress during the third week (21 - 14 days) before first insemination had largest effect on farrowing rate. Heat stress during the period between 7 days before successful insemination until 12 days after successful insemination had largest effect on total born. Correlations between temperatures on consecutive days during these periods were extremely high (> 0.9). Therefore, for farrowing rate the maximum temperature on 21 days before first insemination and for total born the maximum temperature at day of successful insemination can be used as predictive measures of heat stress in commercial sow farms. Additionally, differences between daughter groups of sires were identified in response to high temperatures. This might indicate possibilities for genetic selection on heat tolerance.

Key words: sows, gilts, farrowing rate, total born, heat stress, environmental temperature

4.1 Introduction

Undisturbed piglet production is of great value in the pork supply chain. Farrowing rate is a key factor for consistent piglet production as it affects the number of non-productive sow days per year and the number of litters per sow per year (Bloemhof et al., 2012). In addition, total born has been considered as one of the most important traits in pig breeding programs (Hanenberg et al., 2001).

Seasonal variation has been shown to result in a decreased farrowing rate and an increased weaning to estrus interval (Love et al., 1993; Prunier et al., 1996). Pigs are especially sensitive to elevated ambient temperatures because they have problems with self-thermo regulation. Increased environmental temperatures can lead to reductions in feed intake, milk yield, and overall reproductive performance of sows (Black et al., 1993; Love et al., 1995; Lewis and Bunter, 2011a). Economic losses to the United States swine industry from heat stress were estimated to be $299 million per year (St-Pierre et al., 2003).

In a previous study on the interaction between reproductive performance and heat stress (Bloemhof et al., 2008), sows from a Dutch Yorkshire dam line, were more sensitive to high temperatures than sows from an International Large White dam line. Bloemhof et al. (2008) only considered the maximum temperature on the actual day of insemination as measure of heat stress. However, it is reasonable to hypothesize that heat stress before or after day of insemination will also have a significant impact on reproductive performance. Only when the most heat stress sensitive period(s) during the reproduction cycle are identified suitable management and breeding strategies can be developed. Therefore, the objectives of this study are 1) to investigate what the effect of heat stress during each day of the reproduction cycle of the sow is on farrowing rate and total born, and 2) to identify when this effect on farrowing rate and total born is largest.

4.2 Material and methods

Animal Care and Use Committee approval was not needed for this study because regularly collected data for the TOPIGS breeding program (Vught, The Netherlands) were used. The TOPIGS breeding program operates according to the EFABAR code of conduct (Neeteson et al., 2006).

Reproduction records

Data were sourced from nucleus farms in Spain and Portugal that were breeding purebred Dutch line sows. The Dutch line is a Yorkshire dam line and part of the TOPIGS breeding program (Vught, the Netherlands). Insemination and subsequent farrowing data was available for 32,059 first mating records performed from

January 2003 until December 2010 on 23 farms. Each record included sow identification number, birth date of the sow, parity, farm, date of first insemination in that specific cycle, date of successful insemination, service sire, farrowing date, gestation length, farrowing rate, total born, number of piglets born alive, number of stillborn piglets, weaning date and number of weaned piglets. Farrowing rate on animal level was defined as a binary trait: 1 if the first insemination within a parity resulted in a gestation length longer than 108 days, or if total born from first insemination was at least 1 piglet. Otherwise farrowing rate within a parity was considered as 0. For sows culled after first insemination within a parity because of reproductive failure, farrowing rate was also recorded as 0. Sows culled for other reasons after first insemination, such as leg problems, were removed from the dataset. Total born was recorded immediately after farrowing and was defined as the sum of number of piglets born alive and number of stillborn piglets. Total born ranged from 1 to 30. A gilt in this dataset was defined as a sow with first insemination in parity 1 that never farrowed before. Sows in this dataset refer to sows from second parity up to seventh parity. Observations were removed from the dataset when one of the following traits were larger/smaller than their mean ± 3 × SD: 1) farrowing interval; 2) lactation length; 3) gestation length; 4) number born alive; and 5) number stillborn. Seven farms had less than 250 observations in the dataset and were therefore removed. Observations from sows that originated from a different line than the Dutch Yorkshire dam line were removed from the dataset. After these data editing steps the dataset used for the analysis consisted of 22,750 records from 5,024 sows on 16 farms.

Meteorological data used

Meteorological data were available from the European Climate Assessment Dataset (Klein Tank et al., 2002) and included daily summaries for the maximum, minimum and average outside temperature for 6 Spanish and 3 Portuguese weather stations and were available from January 2003 until June 2011. The closest available weather station was assigned to each farm. Most of the farms had a weather station within 122 km radius of the farm, with the closest being 45 km and the farthest being 209 km. Figure 4.1 shows a map of Spain and Portugal indicating the approximate location of farms and weather stations. Freitas et al. (2006) estimated a correlation of 0.9 between on-farm temperature data and weather station temperature in the USA, even for weather stations more than 300 km from the farm. Therefore, the meteorological data used in the current study should fairly represent the temperature at these farms. Climate in Spain and Portugal is characterized by hot summers and mild winters, humidity is relatively low (< 70%, Klein Tank et al., 2002) and was therefore not considered in the analysis. Gilts and sows were housed in automatically controlled natural ventilated sheds (using wind breaking curtains), without any cooling. Day length in Spain/Portugal on June 21 and December 21 was 13 hours 59 minutes and 8 hours 34 minutes, respectively. Day light in the sheds was admitted through the wind breaking curtains, however also artificial light was available.

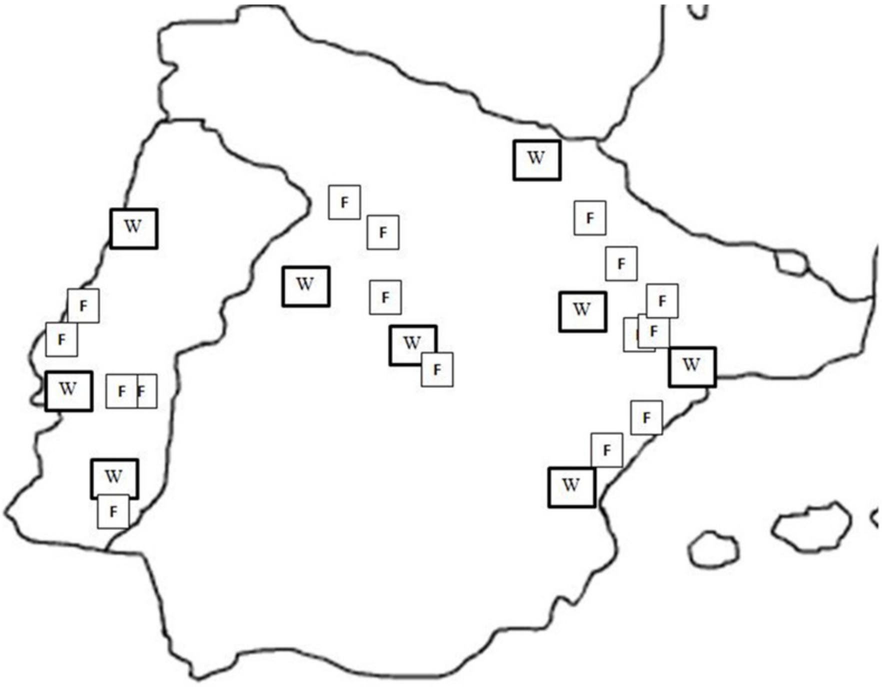


Figure 4.1 Map of Spain and Portugal with the approximate location of the 9 weather stations (identified with W) and the 16 farms (identified with F).

Estimation of heat stress

For farrowing rate, maximum and minimum temperature per day was matched to each day of the sow's cycle from 28 days before day of *first* insemination until 108 days after *first* insemination. For total born maximum and minimum temperature per day was matched to each day of the sow's cycle from 28 days before day of successful (= insemination which resulted in a farrowing) insemination until day of farrowing. Diurnal temperature range was calculated for each day as the difference between maximum temperature and minimum temperature. Heat load for each day was calculated separately for both farrowing rate and total born as: hl = MT – UCT, hl = 0 when MT $\leq$ UCT. Where hl = heat load, MT = maximum temperature on day used for analysis (for example the day of insemination), and UCT = the upper critical temperature. The upper critical temperature (**UCT**) used here relates to the thermo-neutral zone for pig production as described by Bloemhof et al. (2008). When temperature rises above this UCT, the pig has to reduce performance to avoid extra heat production (Bloemhof et al., 2008). To validate the UCT definition from Bloemhof et al. (2008) two additional UCT definitions were studied. Three different UCT definitions were used to calculate heat load for farrowing rate, 1) an UCT of 19.2°C based on the study from Bloemhof et al. (2008); 2) an UCT of 15°C; 3) an UCT of 25°C. Three different UCT definitions were used to calculate heat load for total born, 1) an UCT of 21.7°C based on the study from Bloemhof et al. (2008); 2) an UCT of 15°C; 3) an UCT of 25°C.

Statistical analysis

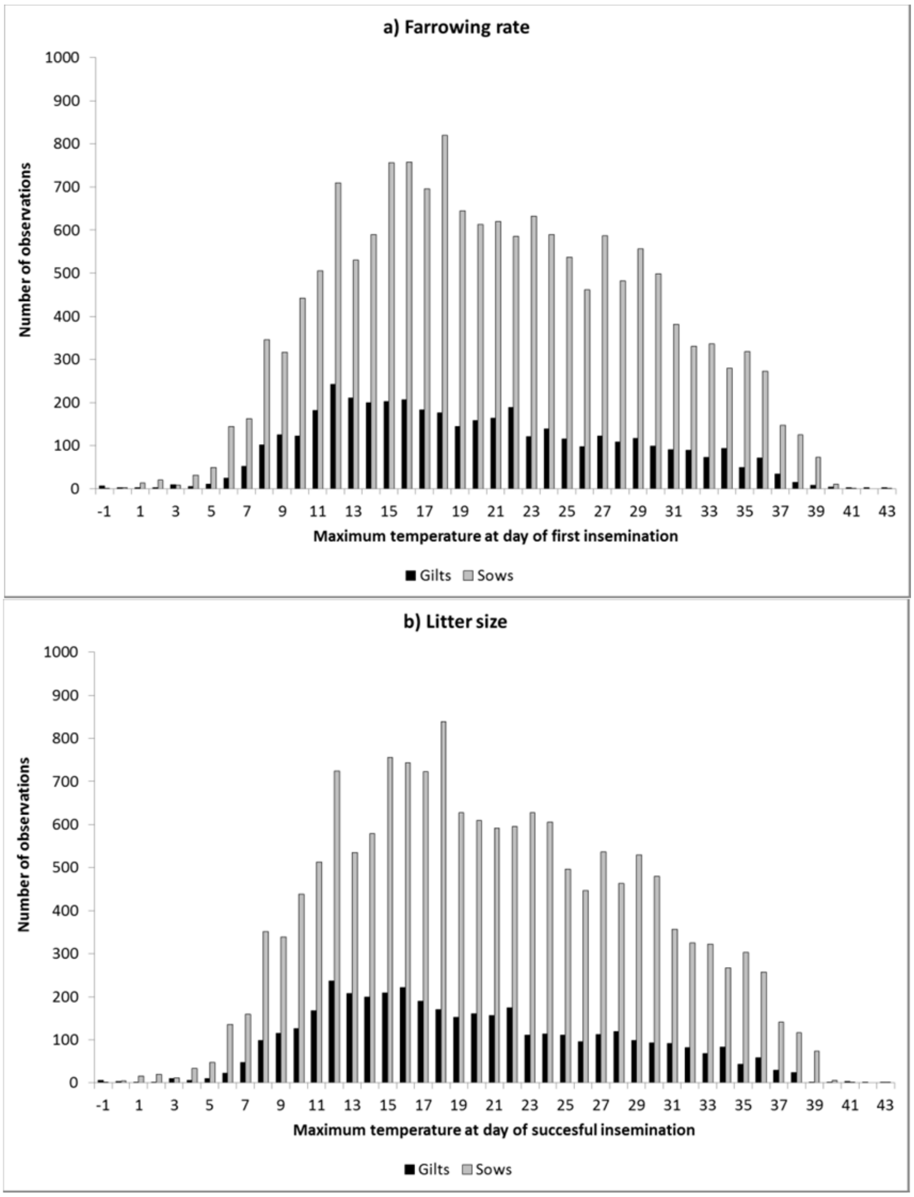
A descriptive analysis was performed for gilts and sows separately using the MEANS procedure in SAS 9.2 (SAS Inst. Inc., Cary, NC). For the descriptive analysis maximum outside temperature was rounded to whole numbers and divided into 26 temperature classes (10°C, 11°C, …, 35°C), means were only calculated when the temperature class had at least 25 observations. Figure 4.2 shows number of observation for each temperature class for gilts and sows separately. Differences in means between gilts and sows were tested for significance using the TTEST procedure in SAS 9.2 (SAS Inst. Inc., Cary, NC).

To identify on which day during the reproduction cycle of the sow heat stress had largest impact on farrowing rate and total born, data were analysed separately for gilts and sows using a three-step approach. First, data were corrected for systematic effects using the GLM procedure in SAS 9.2 (SAS Inst. Inc., Cary, NC) with the model:

$$y_{ijkl} = \mu + herd_i + year_j + herd_i \times year_j + service\ sire_k + e_{ijkl} \qquad [1]$$

where y_{ijkl} is the value of farrowing rate or total born, $herd_i$ is the effect of herd i (16 classes), $year_j$ is the effect of year of insemination j (8 classes) and $herd_i \times year_j$ is the interaction between *herd* and *year*, $service\ sire_k$ is the effect of service sire k (411 classes), and e_{ijkl} is a random residual term. Corrected observations (y^*) for farrowing rate or total born were calculated for each insemination record as:

$$y^* = \hat{\mu} + \hat{e}_{ijkl} \qquad [2].$$


a) Farrowing rate

b) Litter size

Figure 4.2 Number of observations for farrowing rate and total born in relation to maximum temperature for gilts (sows from parity 1) and sows (parity 2-7).

Second, to identify on which day(s) during the reproduction cycle of the sow heat stress had maximum effect on farrowing rate, pairwise Pearson correlations were estimated between the corrected observation (y^*) for farrowing rate and maximum temperature, diurnal temperature range and the 3 heat load variables (based on UCT of 15°C, 19.2°C, and 25°C) at each day of the sow's cycle from 28 days before day of *first* insemination until 108 days after *first* insemination. As temperature might have a different effect on gilts vs. sows the Pearson correlations and standard errors were estimated separately for gilts and sows using the CORRELATION procedure (SAS Inst. Inc., Cary, NC).

Third, to identify on which day(s) during the reproduction cycle of the sow heat stress had maximum effect on total born pairwise Pearson correlations were estimated between the corrected observation (y^*) for total born and maximum temperature, diurnal temperature range and the three heat load variables (based on UCT of 15°C, 21.7°C, and 25°C) for each day of the cycle of the sow from 28 days before day of successful insemination (= insemination which resulted in a farrowing) until day of farrowing. Pearson correlations and standard errors were estimated for gilts and sows using the CORRELATION procedure (SAS Inst. Inc., Cary, NC).

Exploration of opportunities for genetic selection

To explore opportunities for genetic selection, sires of the sows were added to the dataset with only daughters from sires with more than 50 daughters remaining in the dataset. This resulted in a dataset of 12,849 observations. Then for each sire the performance of their daughters for farrowing rate and total born was regressed to the heat load (as in Bloemhof et al., 2008) on the day during the reproduction cycle of the sow with maximum effect as:

$$y_{ijklmno} = \mu + parity_i + herd_j + year_k + herd_j \times year_k + service\ sire_l + sire_m + sire_m \times x_n + e_{ijklmno} \qquad [3]$$

where $y_{ijklmno}$ is the value of farrowing rate or total born, $parity_i$ is the general level of parity i (7 classes), $herd_j$ is the effect of herd j (16 classes), $year_k$ is the effect of year of insemination k (8 classes) and $herd_j \times year_k$ is the interaction between *herd* and *year*, $service\ sire_l$ is the effect of service sire l (361 classes), $sire_m$ is the general level of sire m (33 classes), $sire_m \times x_n$ is the slope of the performance of the daughters from the *m-th* sire when x increases by 1°C, x_n is the heat load (as in Bloemhof et al., 2008) on the day with maximum effect on farrowing rate or total born and $e_{ijklmno}$ is a random residual term. All effects fitted in the model were significant. Based on the b-values resulting from model 3 the sires with the 25% strongest slopes were defined as sensitive, the sires with the 25% lowest slopes were defined as robust. This sire group was then added to each insemination record in the dataset.

To study if the differences in response to high temperatures between the daughters from robust and sensitive sires were significant, the model described by Bloemhof et al. (2008) was applied. Firstly, data were corrected for systematic effects using the GLM procedure (SAS Inst. Inc., Cary, NC) with the model:

$$y_{ijklm} = \mu + parity_i + herd_j + year_k + herd_j \times year_k + service\ sire_l + e_{ijklm} \qquad [4]$$

where y_{ijklm} is the value of farrowing rate or total born, $parity_i$ is the general level of parity i (7 classes), $herd_j$ is the effect of herd j (16 classes), $year_k$ is the effect of year of insemination k (8 classes) and $herd_j \times year_k$ is the interaction between *herd* and *year*, $service\ sire_l$ is the effect of service sire l (361 classes) and e_{ijklm} is a random residual term. Corrected observations (y*) for farrowing rate or total born were calculated for each insemination record as:

$$y^* = \hat{\mu} + \hat{e}_{ijklm} \qquad [5].$$

For the sensitive and robust sire daughter group an average of the corrected observations for farrowing rate and total born was calculated per degree Celsius of maximum outside temperature at the day with maximum effect, resulting from the correlation estimates, using the MEANS procedure (SAS Inst. Inc., Cary, NC) and plotted.

To test if daughters from sensitive sires and robust sires respond differently to high temperatures, corrected observations were analysed by sire group using linear regression models and plateau-linear models. The plateau-linear model was based on the approach by Bloemhof et al. (2008). Corrected observations, resulting from model 5, for farrowing rate or total born were included in both models as dependent variable, and regressed against maximum temperature at the day with maximum effect. The linear model was defined as:

$$y_i^* = int + b \times x_i + e_i \qquad [6].$$

The plateau-linear model [7] was defined as:

$y_i^* = c + e_i$ when $x_i \leq UCT$ and
$y_i^* = int + b \times x_i + e_i$ when $x > UCT$ [7].

Where y_i* is the dependent corrected observation for farrowing rate or total born; int is the intercept; b is the change of y_i* when x_i increases with 1°C; x_i is the maximum temperature on the day with maximum effect; *c* is the constant value of y_i* when farrowing rate or total born of the sow is unaffected by temperature; e_i is the residual; and UCT is the upper critical temperature where temperature starts to affect farrowing rate or total born: $UCT = \frac{(c - i)}{b}$. The linear regression and plateau-linear models were compared for goodness-of fit using an F-test.

4.3 Results

Meteorological data

For the period of time considered, temperature on day of first insemination within a parity ranged from an average daily minimum temperature of 10.5˚C to an average maximum daily temperature of 20.6˚C (Table 4.1). Diurnal temperature range on day of first insemination within a parity was on average 10˚C, the maximum difference between maximum and minimum temperature was 36.5˚C. Temperature on day of successful insemination ranged from an average daily minimum temperature of 10.4˚C to an average maximum daily temperature of 20.4˚C (Table 4.1). Diurnal temperature range on day of successful insemination was exactly similar to diurnal temperature range on day of first insemination within a parity. Approximately 50% of the inseminations were performed on days with a maximum temperature above 20˚C (Figure 4.2).

Table 4.1 Descriptive statistics of meteorological data at day of insemination and day of successful insemination.

	Day of first insemination				Day of successful insemination			
Characteristic	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
Minimum temperature, °C	10.5	6.3	-16.9	26.0	10.4	6.2	-16.9	26
Maximum temperature, °C	20.6	8.1	-2.4	44.1	20.4	8.1	-2.4	43.2
Diurnal temperature range, °C	10.0	4.1	0.0	36.5	10.0	4.1	0.0	36.5

Table 4.2 Descriptive statistics of reproductive data.

	Gilts (parity 1)			Sows (parity 2-7)			Gilts vs Sows	
Characteristic	N	Mean	SD	N	Mean	SD	Difference	P-value
Parity	4,331	1	-	16,556	4.1	±1.6	-	-
Gestation length, days	4,200	113.7	±9.1	16,223	113.9	±6.7	-0.25	0.09
Farrowing rate	4,244	0.79	±0.41	16,298	0.87	±0.34	-0.07	<0.01
Total born	4,111	11.3	±2.7	16,053	12.2	±2.7	-0.84	<0.01

Effect of temperature on farrowing rate and total born in gilts and sows

Differences between gilts and sows with respect to reproduction traits are shown in Table 4.2. As expected, there were hardly any differences in gestation lengths between gilts and sows suggesting similar reproduction cycles. Average farrowing rate of sows was significantly ($P < 0.01$) greater than farrowing rate of gilts; in sows 87% of the first inseminations resulted in a farrowing, whereas this was 79% for gilts. Average total born of sows (12.2 piglets) was almost 1 piglet greater than total born of gilts (11.3 piglets) ($P < 0.01$). Gilts and sows differed in their responses to increasing temperatures. These differences were observed in both farrowing rate and in total born. Means for farrowing rates plotted against maximum temperatures on days of *first* insemination and means for total born plotted against maximum temperatures on days of successful insemination are shown in Figure 4.3. Farrowing rate of gilts was significantly ($P < 0.05$) lower than farrowing rate of sows at almost all temperatures with a slightly larger decrease in farrowing rate of gilts at higher temperatures than for sows. More variation in farrowing rate was shown in gilts than in sows. Figure 4.2 shows the number of records used for the estimates. There were more than 25 insemination records per temperature class, covering a wide range of temperatures from 5°C to 35°C. This suggests that the greater variability in reproductive performance in gilts than in sows was not due to a lower number of observations per temperature class for gilts than for sows. Total born of sows was also significantly ($P < 0.05$) greater than total born of gilts at all temperatures and difference in total born was even greater at higher temperatures (Figure 4.3). In view of these differences further analysis was done separately for gilts and sows.

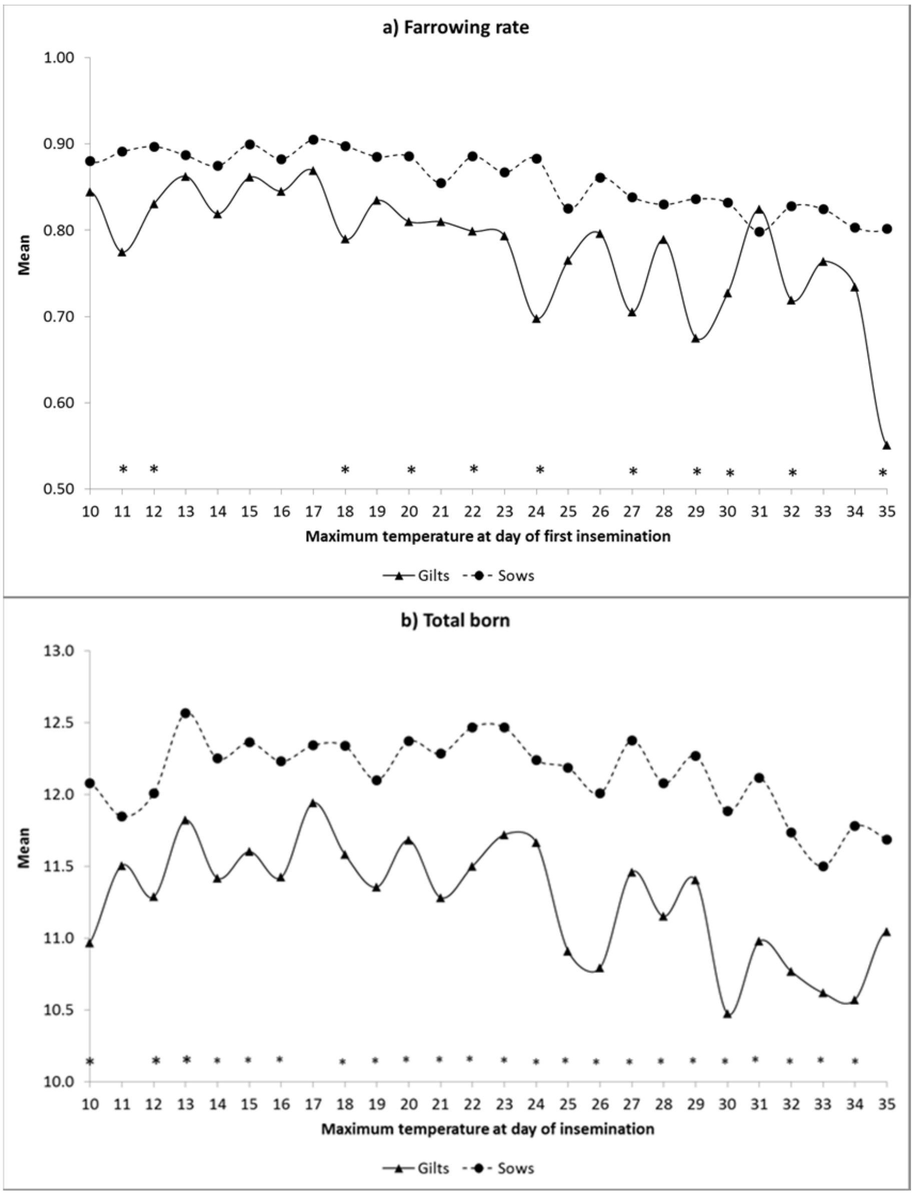
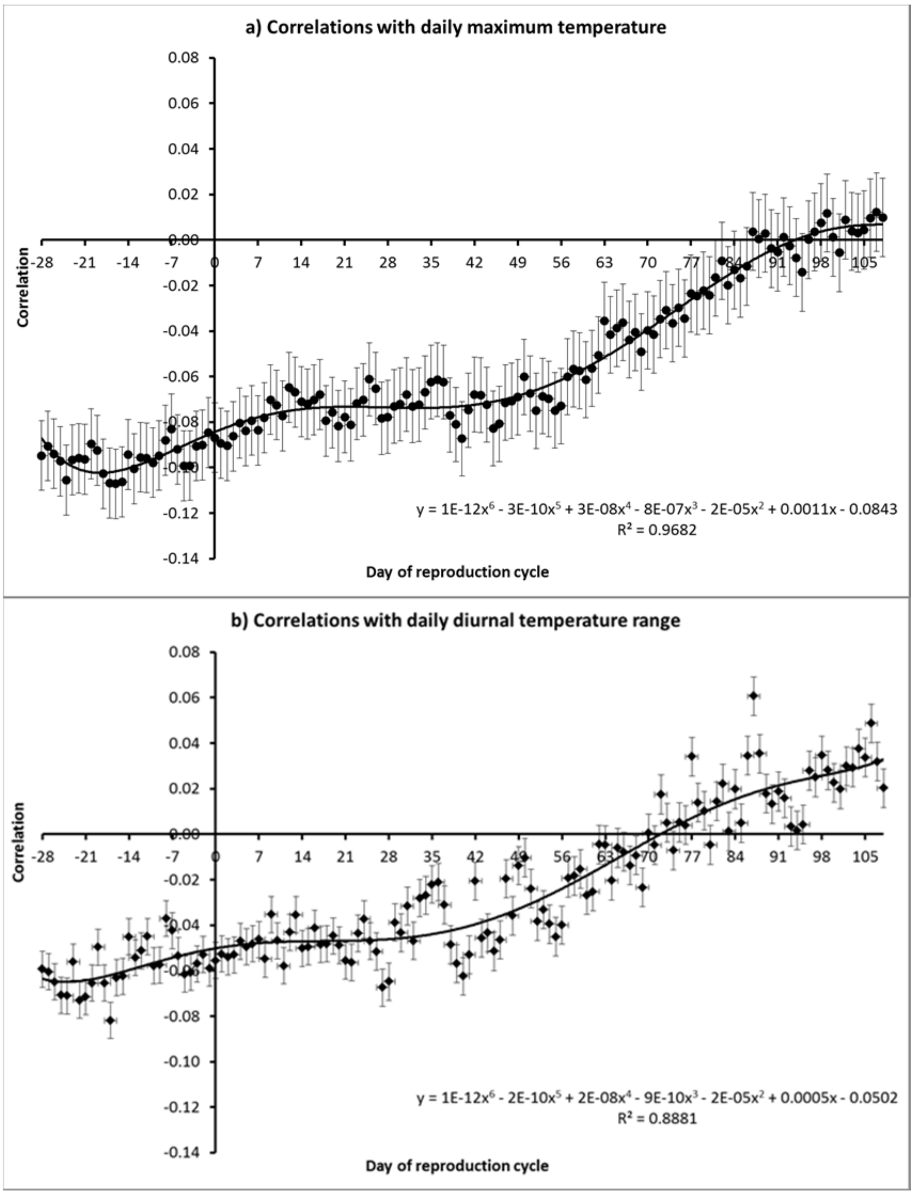


Figure 4.3 Means for farrowing rate and total born per ˚C maximum outside temperature for gilts (sows from parity 1) and sows (parity 2-7). An asterisk (*) indicates significance of difference between gilts and sows within each temperature class.

Relationship between farrowing rate and daily temperature variables

The relationship between farrowing rate and daily temperature variables was evaluated in terms of a Pearson correlation between temperature on a given day of the reproduction cycle and farrowing rate. Main purpose of this analysis was to identify days and periods that had maximum effect on farrowing rate. Estimates of Pearson correlations for gilts with respect to three temperature variables a) maximum daily temperature; b) diurnal temperature range and c) heat load for gilts are shown in Figure 4.4a, 4.4b, and 4.4c, respectively. Estimates ranged from -0.11 ± 0.02 on day 16 before *first* insemination to 0.01 ± 0.02 on day 107 after *first* insemination for daily maximum temperature (Figure 4.4a). It is important to note that the correlation of -0.11 indicates an unfavorable effect of increase in temperature on farrowing rate. The increase in correlations with respect to days of the reproduction cycle was not linear, suggesting distinct periods of greater effects. A sixth degree polynomial function was the best fit to the correlation estimates according to R-squares. According to this function, high temperatures on the days during the third week (21 to 14 days) before *first* insemination had maximum effect on farrowing rate. A second period between 38 days and 55 days after *first* insemination also had a high effect but lower than the period before insemination. The Pearson correlations with respect to daily diurnal temperature range were weaker than those for maximum temperature (Figure 4.4b). They followed similar pattern but periods of strongest effects were less distinct. The effect of heat load was evaluated using three different upper critical temperatures (Figure 4.4c). The estimates of Pearson correlations followed a similar pattern as for daily maximum temperature. Correlations were strongest when UCT was as low as 25°C and were weaker with decreasing UCT. However differences between correlation estimates with different UCT were not significant.


a) Correlations with daily maximum temperature
Correlation
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14
-28
-21
-14
-7
0
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
y = 1E-12x⁶ - 3E-10x⁵ + 3E-08x⁴ - 8E-07x³ - 2E-05x² + 0.0011x - 0.0843
R² = 0.9682
Day of reproduction cycle
b) Correlations with daily diurnal temperature range
Correlation
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14
-28
-21
-14
-7
0
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
y = 1E-12x⁶ - 2E-10x⁵ + 2E-08x⁴ - 9E-10x³ - 2E-05x² + 0.0005x - 0.0502
R² = 0.8881
Day of reproduction cycle

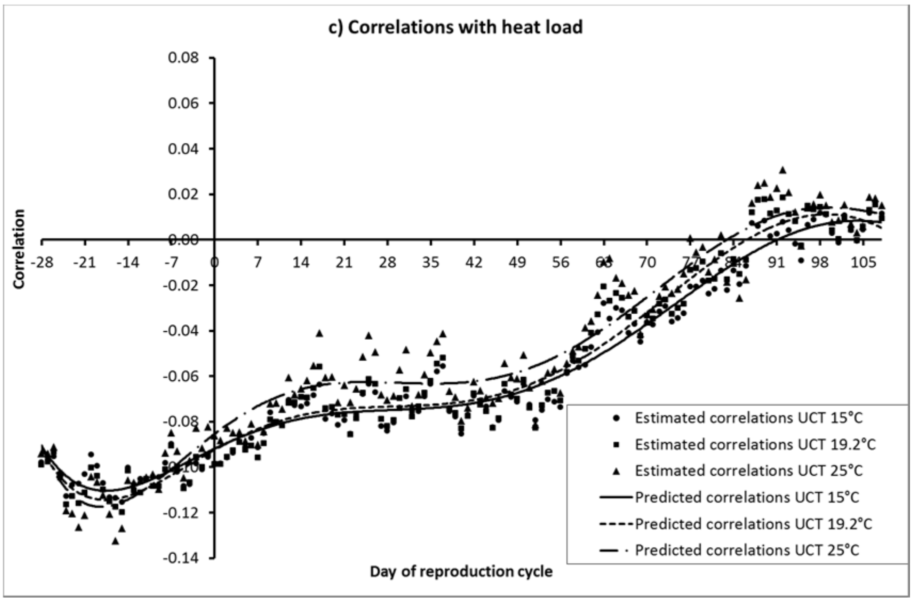
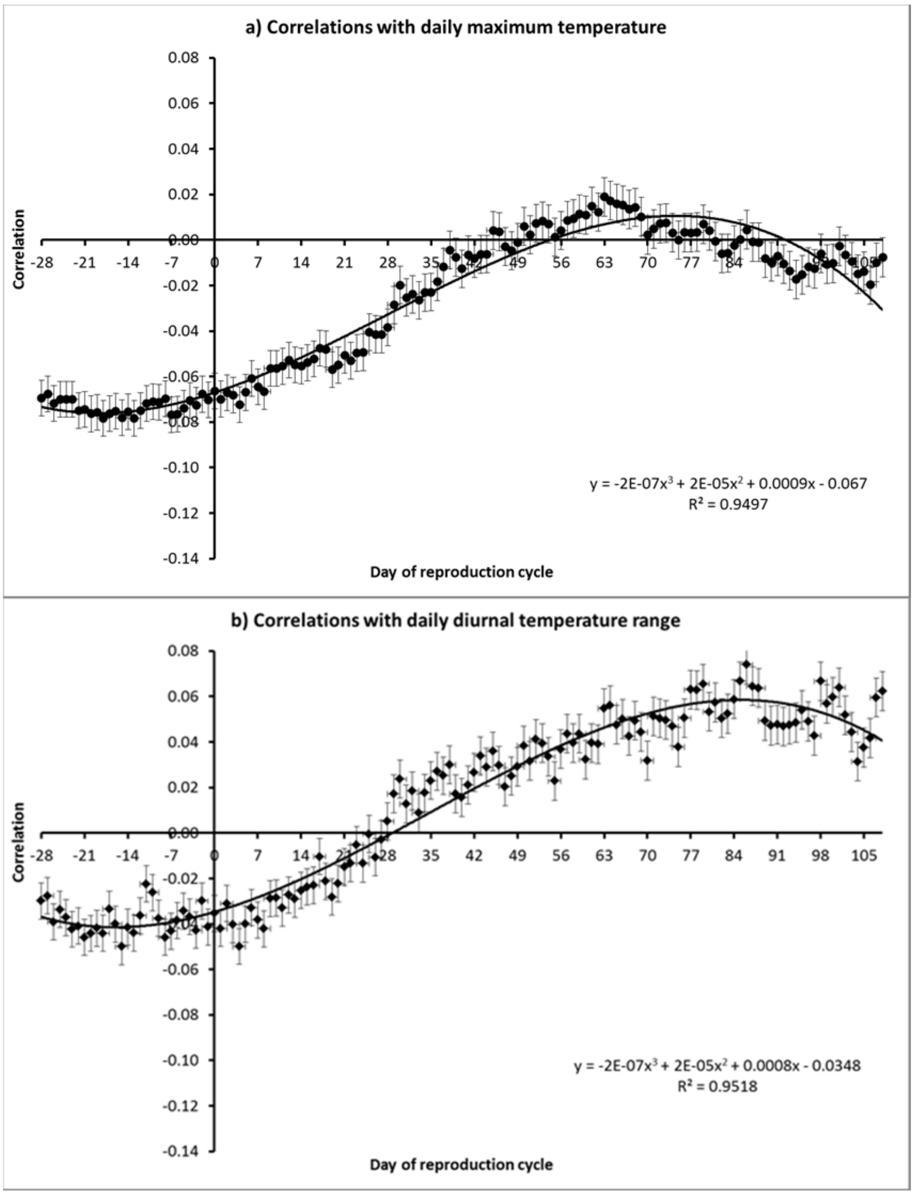


Figure 4.4 Pearson correlations between farrowing rate of gilts (sows from parity 1) and daily temperature variables. Farrowing rate was corrected for the systematic effects of herd, year of insemination, the interaction between herd and year of insemination and service sire. Day 0 was the day of first insemination in a parity. Vertical bars in a) and b) show standard errors of the correlations. Heat load in c) was estimated as deviation from the upper critical temperature (UCT) considering three levels of UCT; i.e. 15°C, 19.2°C, and 25°C. A sixth degree polynomial function was fitted to the correlations.

Estimates of Pearson correlations for sows with respect to farrowing rate and 3 temperature variables a) maximum daily temperature; b) diurnal temperature range; and c) heat load are shown in Figure 4.5a, 4.5b, and 4.5c, respectively. Considering daily maximum temperature as the effect variable, the correlation estimates ranged from -0.08 ± 0.01 on day 18 before *first* insemination to 0.02 ± 0.01 on day 63 after *first* insemination (Figure 4.5a). The negative but stronger correlation indicates that increasing temperatures in the period before *first* insemination have largest effect on farrowing rate. A majority of the correlations were negative but some of them were positive especially after the 56th day after *first* insemination. A third degree polynomial function was the best fit to the relationship between correlation estimates and days of the reproduction cycle according to its R-square. According to this polynomial function, heat stress during 21 and 14 days (third week) before *first* insemination had largest impact on farrowing rate of sows.


a) Correlations with daily maximum temperature
Correlation
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14
-28 -21 -14 -7 0 7 14 21 28 35 42 49 56 63 70 77 84 91 98 105
y = -2E-07x³ + 2E-05x² + 0.0009x - 0.067
R² = 0.9497
Day of reproduction cycle
b) Correlations with daily diurnal temperature range
Correlation
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14
-28 -21 -14 -7 0 7 14 21 28 35 42 49 56 63 70 77 84 91 98 105
y = -2E-07x³ + 2E-05x² + 0.0008x - 0.0348
R² = 0.9518
Day of reproduction cycle

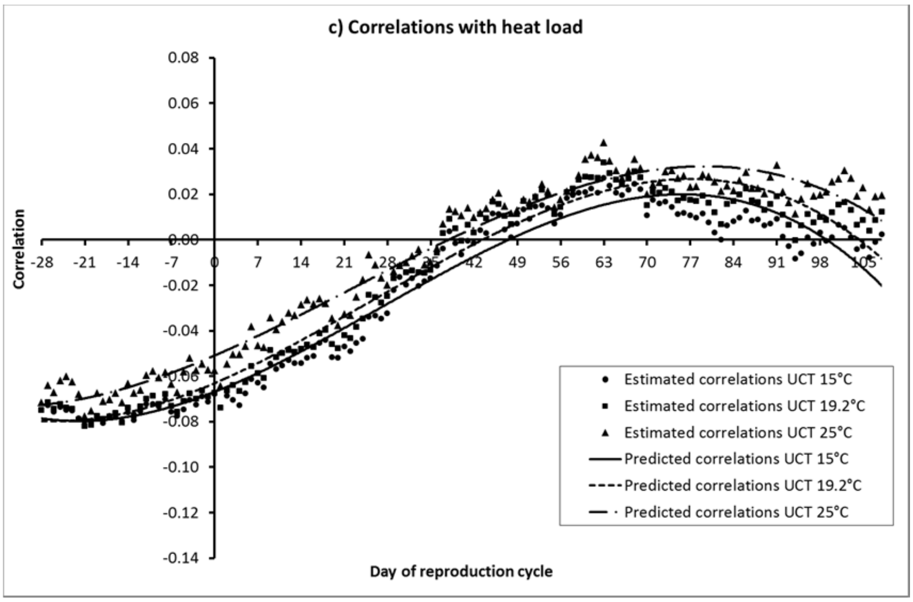
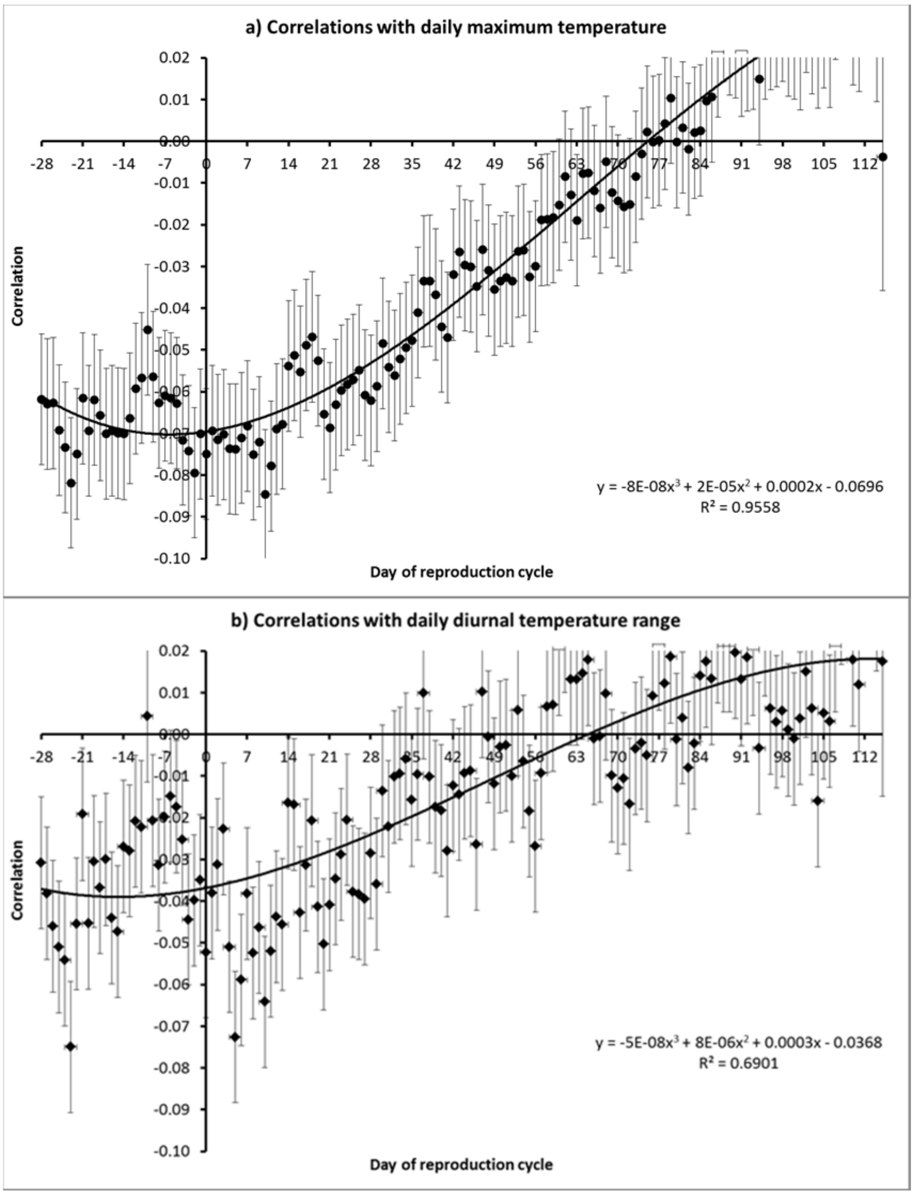


Figure 4.5 Pearson correlations between farrowing rate of sows (parity 2-7) and daily temperature variables. Farrowing rate was corrected for the systematic effects of herd, year of insemination, the interaction between herd and year of insemination and service sire. Day 0 was the day of first insemination in a parity. Vertical bars in a) and b) show standard errors of the correlations. Heat load in c) was estimated as deviation from the upper critical temperature (UCT) considering three levels of UCT; i.e. 15°C, 19.2°C, and 25°C. A third degree polynomial function was fitted to the correlations.

Estimates of Pearson correlations between daily diurnal temperature range and farrowing rate (Figure 4.5b) were weaker than those between maximum temperature and farrowing rate (Figure 4.5a) but followed similar pattern. For sows also the effect of heat load was evaluated using three different upper critical temperatures (Figure 4.5c). Correlations were weakest between farrowing rate and UCT 25°C and strongest between farrowing rate and UCT 15°C but correlations between UCT 19.2°C and farrowing rate were quite similar to correlations between UCT 15°C and farrowing rate.


a) Correlations with daily maximum temperature
Correlation
0.02
0.01
0.00
-0.01
-0.02
-0.03
-0.04
-0.05
-0.06
-0.07
-0.08
-0.09
-0.10
-28 -21 -14 -7 0 7 14 21 28 35 42 49 56 63 70 77 84 91 98 105 112
y = -8E-08x³ + 2E-05x² + 0.0002x - 0.0696
R² = 0.9558
Day of reproduction cycle
b) Correlations with daily diurnal temperature range
Correlation
0.02
0.01
0.00
-0.01
-0.02
-0.03
-0.04
-0.05
-0.06
-0.07
-0.08
-0.09
-0.10
-28 -21 -14 -7 0 7 14 21 28 35 42 49 56 63 70 77 84 91 98 105 112
y = -5E-08x³ + 8E-06x² + 0.0003x - 0.0368
R² = 0.6901
Day of reproduction cycle

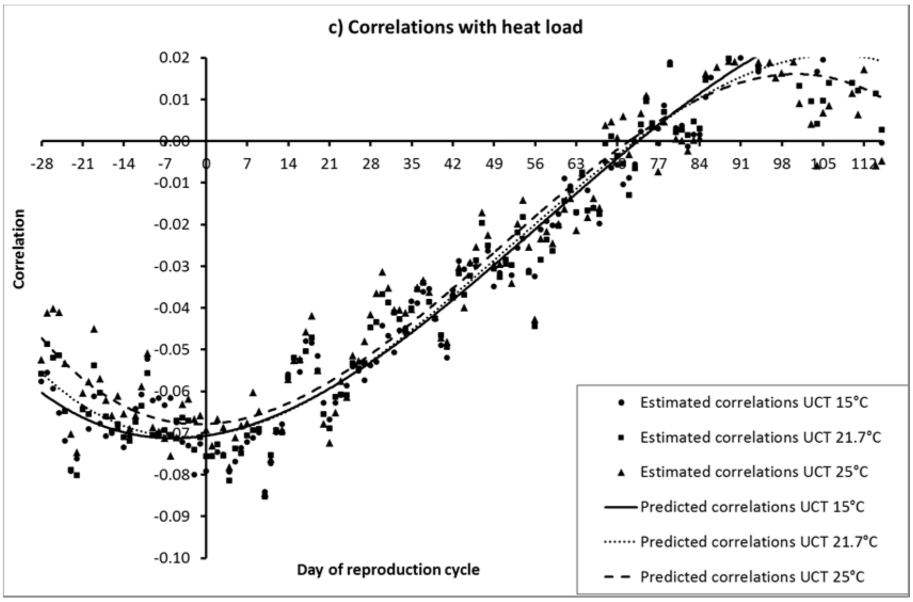
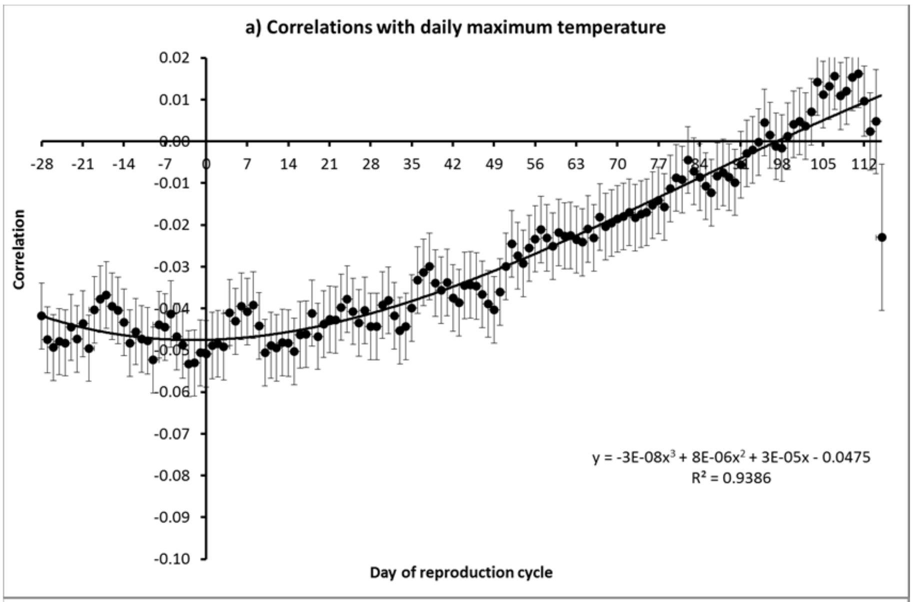


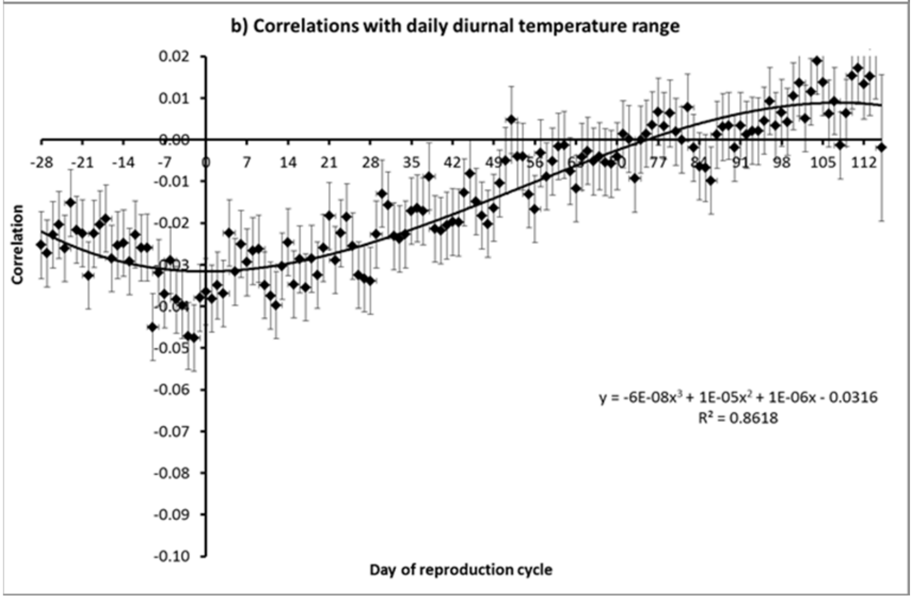
Figure 4.6 Pearson correlations between total born of gilts (sows from parity 1) and daily temperature variables. Total born was corrected for the systematic effects of herd, year of insemination, the interaction between herd and year of insemination and service sire. Day 0 was the day of successful insemination in a cycle. Vertical bars in a) and b) show standard errors of the correlations. Heat load in c) was estimated as deviation from the upper critical temperature (UCT) considering three levels of UCT; i.e. 15°C, 21.7°C, and 25°C. A third degree polynomial function was fitted to the correlations.

Relationship between total born and daily temperature variables

The analysis to identify days and periods of heat stress that had maximum effect on total born of gilts was carried out using Pearson correlations. Again, the changes in these correlations during different days of reproduction cycle were examined with respect to maximum daily temperature, diurnal temperature range as well as heat load. The results are given in Figure 4.6a, 4.6b, and 4.6c, respectively. In this analysis, day 0 of the reproduction cycle was the day of successful insemination that led to the total born rather than the day of *first* insemination as in case of farrowing rate. In general, correlations were smaller in magnitude than those for farrowing rate. Estimates of correlations ranged from -0.08 ± 0.02 on 10th day after insemination to 0.05 ± 0.02 on 109 days after day of successful insemination (Figure 4.6a). A third degree polynomial function was found to be the best fit to the correlation estimates. According to this function high temperatures during the period between day of successful insemination and 14 days after successful insemination had the strongest effect on total born of gilts. The Pearson correlations with respect to daily diurnal temperature range were more variable than those for maximum temperature (Figure 4.6b). The effect of heat load (Figure 4.6c) followed similar patterns as for daily maximum temperature, however correlations between heat load and total born were stronger. Strongest correlations between total born of gilts and daily heat load were estimated with heat load based on an UCT of 21.7°C, which was according to Bloemhof et al. (2008) the UCT for total born.

Correlations with respect to total born and maximum daily temperature, diurnal temperature range and heat load for sows are given in Figure 4.7a, 4.7b, and 4.7c respectively. Estimates of Pearson correlations ranged from -0.05 ± 0.01 on day 3 before day of successful insemination to 0.02 ± 0.01 on day 111 after day of successful insemination (Figure 4.7a). According to the third degree polynomial function, high temperatures in the period from 7 days before successful insemination until 12 days after successful insemination have largest effect on total born. The correlations with respect to total born and diurnal temperature range followed the same pattern as for maximum temperature however estimates were somewhat weaker than with maximum temperature (Figure 4.7b). Correlations between total born and daily heat load followed similar pattern as for daily diurnal temperature range but the periods of high effects were more distinct (Figure 4.7c).


a) Correlations with daily maximum temperature
Correlation
0.02
0.01
0.00
-0.01
-0.02
-0.03
-0.04
-0.05
-0.06
-0.07
-0.08
-0.09
-0.10
-28
-21
-14
-7
0
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
112
y = -3E-08x³ + 8E-06x² + 3E-05x - 0.0475
R² = 0.9386
Day of reproduction cycle


b) Correlations with daily diurnal temperature range
Correlation
0.02
0.01
0.00
-0.01
-0.02
-0.03
-0.04
-0.05
-0.06
-0.07
-0.08
-0.09
-0.10
-28
-21
-14
-7
0
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
112
y = -6E-08x³ + 1E-05x² + 1E-06x - 0.0316
R² = 0.8618
Day of reproduction cycle

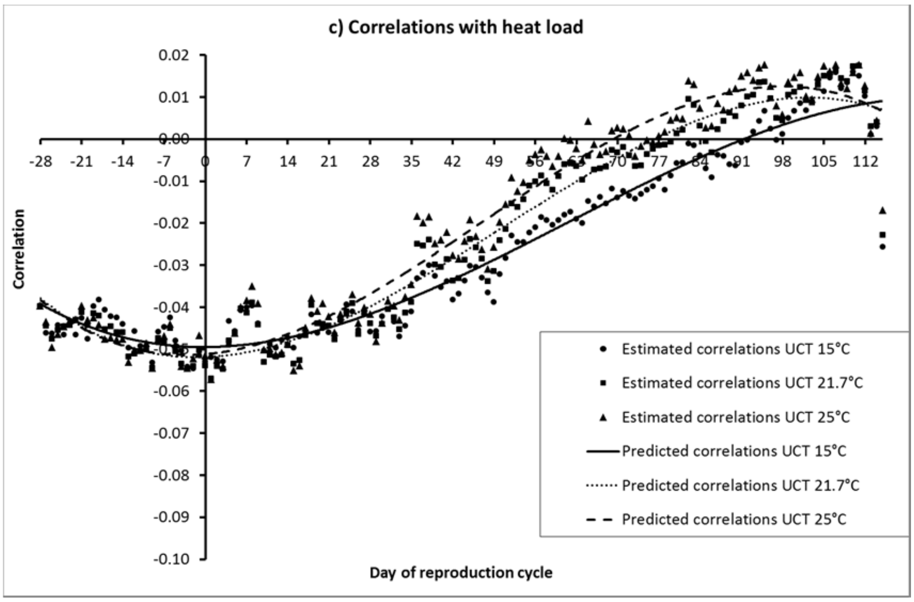


Figure 4.7 Pearson correlations between total born of sows (parity 2-7) and daily temperature variables. Total born was corrected for the systematic effects of herd, year of insemination, the interaction between herd and year of insemination and service sire. Day 0 was the day of successful insemination in a cycle. Vertical bars in a) and b) show standard errors of the correlations. Heat load in c) was estimated as deviation from the upper critical temperature (UCT) considering three levels of UCT; i.e. 15°C, 21.7°C, and 25°C. A third degree polynomial function was fitted to the correlations.

Exploration of opportunities for genetic selection

In addition to the analysis to identify days during the reproduction cycle that had maximum effect on farrowing rate or total born, a preliminary analysis was conducted to evaluate the expected effect of genetic selection of sires based on the heat load on a given day. The purpose was to explore if there are any opportunities for selection of sires and dams to improve the farrowing rate or total born in the next generation based on heat tolerance. In case of farrowing rate, the temperature on the 21st day before *first* insemination was considered to classify the sires into sensitive, and robust categories using model 4.

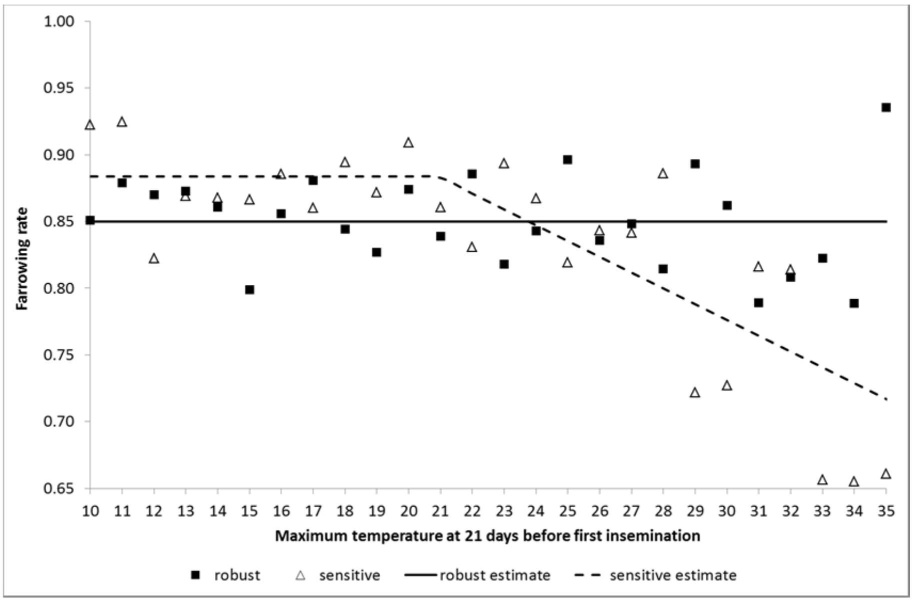


Figure 4.8 Means for farrowing rate (corrected for the systematic effects of parity, herd, year of insemination, the interaction between herd and year of insemination and service sire) in relation to maximum temperature on the 21st day before *first* insemination for daughters from sires grouped according to their sensitivity or robustness to high temperatures. The symbols show the corrected daughter averages for each temperature class and the lines show the significant estimated effect of maximum temperature on the 21st day before *first* insemination on farrowing rate for daughters from robust and sensitive sires.

The average farrowing rates of the daughters of the sensitive or robust sires with respect to the maximum temperature on this day are given in Figure 4.8 as well as the significant model of best fit, either the plateau-linear or linear model. Differences in response to high temperatures were found when applying the plateau-linear model to farrowing rate of daughters of sensitive or robust sires. For daughters of robust sires no effect of temperature on farrowing rate could be estimated (Figure 4.8). A plateau-linear relationship was observed for farrowing rate of daughters of sensitive sires (Figure 4.8), the estimated UCT was 20.9°C and farrowing rate dropped 1% per °C above the UCT. Resulting at 30°C in an estimated average farrowing rate of 78% for daughters of the sensitive sires compared to an average estimated farrowing rate of 85% for daughters of robust sires. In case of total born, maximum temperature at day of successful insemination was considered for classification of the sires into sensitive and robust categories using model 4, the results are shown in Figure 4.9.

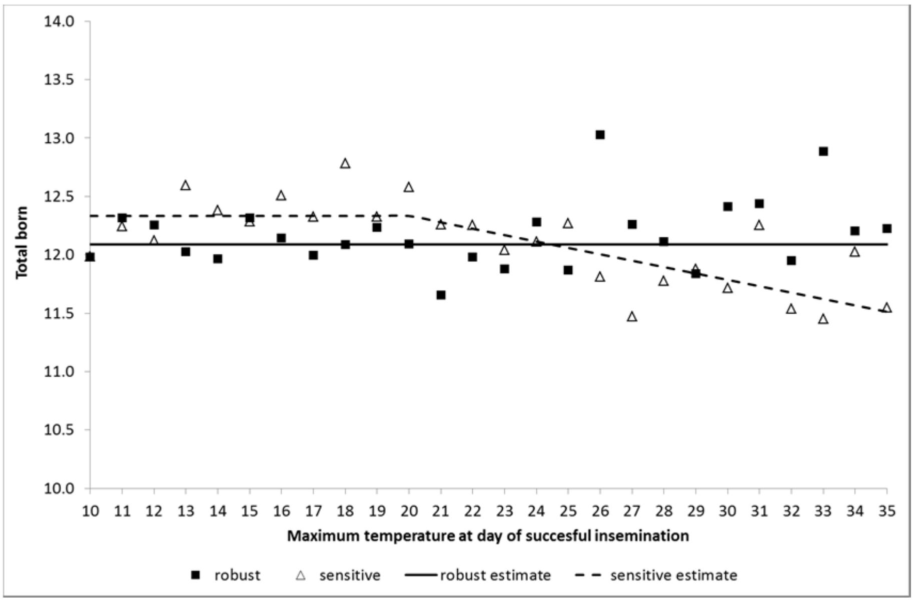


Figure 4.9 Means for total born (corrected for the systematic effects of parity, herd, year of insemination, the interaction between herd and year of insemination and service sire) in relation to maximum temperature at day of successful insemination for daughters from sires grouped according to their sensitivity or robustness to high temperatures. The symbols show the corrected daughter averages for each temperature class and the lines show the significant estimated effect of maximum temperature at day of successful insemination on total born for daughters from robust and sensitive sires.

Again no effect of temperature on total born of daughters from robust sires could be estimated. A plateau-linear relationship was significantly the best fit for total born of daughters of sensitive sires (Figure 4.9), the estimated UCT was 20°C and total born dropped with 0.05 piglet per °C above the UCT. Even though total born of daughters of robust sires was lower than total born of daughters of sensitive sires when temperature was below 25°C, above 25°C total born of daughters of robust sires was greater than total born of daughters of sensitive sires.

4.4 Discussion

This study shows that heat stress during 21-14 days prior to *first* insemination has largest effect on farrowing rate of gilts and sows. Heat stress in the period between 7 days before successful insemination until 12 days after had largest impact on total born. Differences between daughter groups of sires were identified in response to high temperatures. This might indicate possibilities for genetic selection on heat tolerance.

Differences between gilts and sows in their responses to heat stress

Farrowing rate of sows was on average 8% greater than farrowing rate of gilts, 87% and 79%, respectively. Gilts are typically in the growth phase and not completely mature. Therefore, low farrowing rate in gilts might be caused by immaturity of the endocrine system of gilts compared to the endocrine system of older sows. Koketsu et al. (1997) suggested that the level of circulating progesterone produced by the corpora lutea of gilts is lower than in sows. The level of progesterone directly influences pregnancy maintenance and embryonic survival (Jindal et al., 1996; Athorn et al., 2011). Immaturity of the endocrine system in gilts might have resulted in pregnancy disruption (Koketsu et al., 1997) and lower farrowing rate.

Total born in sows was almost 1 piglet greater than in gilts, which could be expected because many studies have observed the lowest total born in gilts and a maximum total born in parity 3-5 sows (e.g., Quesnel et al., 2008). Basically, sows are a selected subset of farrowed gilts that have not been culled due to reproductive failure and other problems after the first parity. Approximately 15-20% of sows are culled after producing only 1 litter (Lopéz-Serrano et al., 2000; Engblom et al., 2007; Koketsu, 2007). This partly explains the differences in farrowing rate and total born between gilts and sows, as the main culling reason of gilts is reproductive failure or low productivity (Engblom et al., 2007).

Correlations between temperature and reproductive outcomes (farrowing rate or total born) were stronger in gilts than in sows. This implies that heat stress has a stronger effect on reproductive performance of gilts than of sows. According to Tummaruk et al. (2010) farrowing rate of gilts is more affected by high temperatures than farrowing rate of sows. The main difference between gilts and sows is that sows have been lactating before being inseminated, which is not the case for gilts. This means that the physiological status is very different between gilts and sows. Additionally, gilts are still growing to their mature size. Their growth increases metabolic rate (Bastianelli and Sauvant, 1997), and this makes gilts more sensitive to heat stress than sows. Next to growth, it can be hypothesized that gilts differ from older parity sows in the fact that producing a first litter (the act of gestation) might be a stressor in itself. Pigs have been shown to be sensitive to novel environments, situations and novel changes within themselves that cause disruption to their internal environment and this could have significant production outcomes (Lewis et al., 2008). Therefore it can be hypothesized that producing a first litter and the internal changes within the gilt associated with that, might make the gilt even more sensitive to heat stress.

Usefulness of different measures of heat stress

Maximum temperature, diurnal temperature range and heat load were compared for their usefulness as measure of heat stress. The correlations were greatest for maximum temperature, followed by those for heat load and diurnal temperature range. Therefore, maximum temperature can be considered as the most important heat stress descriptor for as well farrowing rate as total born. This also suggests that gilts and sows are more sensitive to peaks in temperature than to differences between temperatures during day and night or chronic periods of high temperatures.

The correlations between the three heat load definitions and farrowing rate or total born followed similar pattern as for daily maximum temperature. This was expected as heat load is the difference between maximum temperature and UCT. Among the three definitions of heat load, correlations were stronger with lower values for UCT. However, differences in correlations between a UCT of 15°C and the UCT of 19.2°C or 21.7°C, as estimated by Bloemhof et al. (2008), were not very large.

Pigs encounter heat stress when temperature exceeds the UCT of the thermo-neutral zone. This zone is based on the body temperature of the pig and is the range of ambient temperatures between the lower and upper critical temperature (Bianca, 1976). However, one could argue that there is a lower and upper critical temperature for pig performance (Bloemhof et al., 2008). Below the lower critical temperature, the performance is reduced due to greater requirement for maintaining body temperature. When temperature rises above the UCT, the pig has to reduce performance to avoid extra heat production (Bloemhof et al., 2008). As pig production is expanding more and more in regions with hot climates such as Latin America and South and East Asia (FAO, 2006) and temperature is expected to increase globally as a result of climate change (Hoffmann, 2010), heat stress will become even more important and could be a limiting factor for pig production. Bloemhof et al. (2008) used a plateau-linear model to estimate upper critical temperatures for farrowing rate and total born for an International Large White line and a Dutch Yorkshire line. The data used for the current study is an extension of the data used by Bloemhof et al. (2008). According to the results shown in the current study the upper critical temperature of 19.2°C for farrowing rate and 21.7°C for total born seem to be still valid in the Dutch Yorkshire population.

There has been limited success in identifying the relation between reproductive traits and humidity. Suriyasomboon et al. (2006) showed some negative effects of increased humidity on total born in Thailand, however results were not consistent over farms. However, Lewis and Bunter (2011a) found no effect of humidity on reproduction in a climate zone which was characterized by low relative humidity. Therefore, in the current study humidity was not considered as humidity in Spain and Portugal is in general not high.

Effects of heat stress in different periods during reproduction on farrowing rate

High temperatures 21 - 14 days prior to *first* insemination show largest effect on farrowing rate of sows and gilts (Figure 4.4 and Figure 4.5). This period coincides with the previous estrous and start of the new estrous cycle for gilts and the start of the lactation period of sows. The greater effect of heat stress during the lactation could be partly related to reduced feed intake. Several studies have reported that high temperatures during lactation period result in a decreased feed intake (Black et al., 1993; Lewis and Bunter, 2011a; Bergsma and Hermesch, 2012). At the same time, there is an increase in follicle development during the lactation phase (Kunavongkrit et al., 1982). Lower levels of feed intake could lead to reduction in the release of Luteinizing Hormone during lactation, resulting in reduced follicle development during and after lactation (Quesnel et al., 1998). Reduced follicle development results in lower ovulation rates and reduced oocyte quality and follicular fluid which results in increased embryonic mortality (Kemp et al., 2006). Low ovulation rate, poor oocyte quality and high embryonic mortality may result in low number of embryos (Bertoldo et al., 2012). For maternal recognition at day 12 of gestation, at least 2 viable embryos in each uterine horn are needed (Senger, 1999). When this threshold is not reached, the sow returns to estrus resulting in decreased farrowing rate.

For gilts a second period with strong effect on farrowing rate was observed (Figure 4.4). High temperatures during 38 - 55 days after *first* insemination affect farrowing rate of gilts negatively. However it is hard to relate this period to any physiological process. To allow pregnancy after fertilization, pregnancy recognition by the sow is required. Pregnancy recognition in the gilt and sow happens as a biphasic embryonic signal on days 12 and 18 of gestation (Bertoldo et al., 2012). The second embryonic signal at day 18 is needed for maintenance of the gestation after day 30

(Peltoniemi et al., 2000). Hence, this second period of greater correlation did not coincide with these physiological expectations. On the other hand the period between 21 - 14 days prior to *first* insemination has a stronger effect and could be used as a precaution prior to insemination.

Effects of heat stress in different periods during reproduction on total born

Total born of sows and gilts was affected most by high temperatures during the period of 7 days before successful insemination until 12 days after. The greatest effect was that of the 10th day following insemination. The temperature on the day of insemination is also highly correlated with the 10th day after and other days in this period. Hence, temperature on the day of successful insemination could also be considered as a single day with greatest effect on total born.

The results are in agreement with the study of Omtvedt et al. (1971) which reported that heat stress during the first 2 weeks after mating decreases conception rate and total number of viable embryos. Also in the present study, there was a strong effect of temperature on the 10th day after mating. Lewis and Bunter (2011a) also reported from commercial data that high temperatures on 10th day after mating affected total born and number born alive negatively. Day 10 after mating coincides with the interval of pregnancy recognition and embryonic implantation which occurs around day 12 after insemination (Senger, 1999). Magnitude of correlations between farrowing rate and heat stress were larger than correlations between total born and heat stress. This implies that heat stress affects farrowing rate more than total born. Seasonal disruption of gestation has in generally been related to reduced farrowing rate (Peltoniemi et al., 2000) and less to reduced total born.

Opportunities for optimizing farrowing rate and total born under heat stress

One of the intentions of the current study was to optimize models for estimation of genetic parameters and genetic evaluations using heat stress e.g., as used by Bloemhof et al. (2012). In that study genetic variation in heat stress tolerance was identified for farrowing rate of sows, using maximum temperature at day of insemination as heat stress factor. However, it is reasonable to hypothesize that heat stress before or after day of insemination could also have a significant effect on farrowing rate and total born. Identification of the most effective heat stress factor should result in more accurate estimation of genetic variation for heat stress tolerance in farrowing rate and total born.

Previously differences between dam lines were found in the relationship between temperature and reproductive performance traits (Bloemhof et al., 2008). It was observed that the Dutch line was sensitive to increasing temperatures, and an International Large White line was robust and had very little effect of increasing temperatures beyond the thermo-neutral zone on farrowing rate and total born. Genetic selection within a line might be possible as well. In that case differences among families might be an indication for genetic variation between animals and provide an indication of the opportunities for genetic selection of more robust animals. Therefore, sires were ranked as being sensitive or robust based on regression of reproductive performance of their daughters on heat load.

Farrowing rate of daughters of robust sires was not affected by temperature. Conversely, farrowing rate of daughters of sensitive sires decreased by 1 percentage point per degree Celsius when temperature exceeded 21°C. Their farrowing rate was more than 10% lower than farrowing rate of daughters of robust sires when the temperature reached 32°C. These results suggest that genetic differences with respect to the response to heat stress do exist in the dam line investigated. The pattern is also similar to the one observed by Bloemhof et al. (2008) regarding line differences beyond the upper critical temperature.

Total born of daughters of sensitive sires decreased when temperature exceeded 20°C. In contrast total born of daughters from robust sires was constant regardless of temperature at day of successful insemination. Therefore even though daughters of sensitive sires had larger total born under temperate conditions, daughters of robust sires were superior to daughters of sensitive sires when outside temperatures at day of successful insemination exceeded 25°C.

The rather undisturbed performance of daughters of robust sires regardless of temperature is consistent with the results of Bloemhof et al. (2008) for an International Large White dam line and the results of Lewis and Bunter (2011a) for an Australian Large White dam line as well as a Landrace dam line. Bloemhof et al. (2008) and Lewis and Bunter (2011a) suggested that the absence of a relationship between temperature and reproduction reflected the history of selection in these dam lines in hotter climates. The current study is based on a Dutch Yorkshire dam line, which has been selected on reproductive performance mainly in the Netherlands that has a temperate climate and the temperatures remain therefore below UCT during most part of the year. The differences between daughter-groups described here might be an indication that even though the Dutch Yorkshire dam line was selected in a temperate climate, there is still genetic variation for heat tolerance expressed in reproductive performance.

The above results suggest that selection of sires and dams based on their reaction to heat load could be used to produce progeny with minimum disturbance in farrowing rate and total born under high temperatures. Proper genetic selection will require estimation of heritability under heat load, genetic correlations with other traits and genetic evaluations possibly using individual animal models. The present study has identified the days and periods in which heat stress has maximum effects on farrowing rate and total born for use in the models for these heritability estimates. The periods identified in the present study can also be used to optimize management under heat stress. For example, one could consider cooling the barn during the third week prior to insemination for better farrowing rate and during the week of insemination and one week after that to increase total born if the temperatures rise above 20°C.

Conclusion

The key period during the reproduction cycle of the sow is 21 - 14 days prior to *first* insemination for farrowing rate. Heat stress during this period has largest impact on farrowing rate. For total born, heat stress in the period between 7 days before successful insemination until 12 days after had largest impact on total born. Correlations between temperatures on consecutive days were extremely high (> 0.9). Therefore, for ease of interpretation for farrowing rate the maximum temperature on 21 days before *first* insemination and for total born the maximum temperature at day of successful insemination can be used as predictive measures of heat stress in commercial farms.

4.5 Acknowledgements

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5

Genetics of problem free sow production under heat challenged conditions

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In preparation

Abstract

The pork supply chain is built around productivity in many areas of pig production including sow efficiency. To optimize sow efficiency and productivity a new trait called problem free sow production (**PFSP**) by parity was proposed. The new trait complex incorporates the traits interval weaning first insemination, non-return rate, farrowing rate, and selection for next parity. The objective of this study was to estimate 1) genetic variation for PFSP and its component traits 2) genetic correlations between PFSP, its component traits and sow reproduction traits 3) genetic correlation between PFSP in temperate and heat challenged conditions. Estimates were based on 22,759 insemination records from 4,398 Dutch purebred Yorkshire sows, from January 2002 until December 2011 raised in Spain and Portugal. Problem free sow production was defined as 1 when the sow was inseminated within 7 days after weaning, non-return rate was 1, farrowing rate was 1 and the sow had an insemination in the next parity. If one of these criteria was not met then PFSP was 0. Average level of PFSP was 0.61, implying that 39% of sows do not remain problem-free within a parity. Heritability estimate for PFSP was 0.06 ± 0.01. Genetic correlations between PFSP and general sow reproduction (litter traits) were close to zero, implying that PFSP and sow reproduction can be simultaneously improved via genetic selection. In heat challenged conditions PFSP was 8% lower ($P < 0.01$) than in temperate conditions. Heritability of PFSP in heat challenged conditions was overall 0.03 higher than heritability of PFSP in temperate conditions (0.08 ± 0.01 and 0.05 ± 0.01, respectively). Genetic correlation between PFSP in heat challenged and temperate conditions was high (> 0.9), which implies that PFSP can be considered the same trait in these two environments. Problem free sow production is a trait which can be improved via genetic selection which will result in a reduction of non-productive sow days, in sows that require fewer farmer interventions and ultimately result in an increased number of litters per sow per year.

Key words: sow, reproduction, non-productive sow days, genetics, problem free production

5.1 Introduction

The pork supply chain is built around productivity in many areas of pig production including sow efficiency. Sow productivity depends on a number of related traits, such as litters per sow per year, number of weaned piglets per sow per year and length of productive life. Traditionally pig breeding programs have improved sow productivity by focusing on increasing number weaned piglets per sow per year by selection on total born (Dekkers et al., 2011). To improve herd-level litters per sow per year we propose here a new trait called problem free sow production (**PFSP**) by parity, which incorporates the traits interval weaning first insemination, non-return rate, farrowing rate, and selection for next parity.

Globally, swine herd sizes are increasing and amount of available labour per sow is decreasing (Eurostat, 2010). This requires sows which need less management intervention and which are easier to manage. It is postulated that breeding for improved PFSP can therefore be beneficial for modern swine herds. Before including a new trait in a pig breeding program it is prudent to understand the genetic variation, and the relationship with other traits in the breeding goal. Therefore, the relationship between PFSP and sow reproduction traits needs to be determined.

Currently, the number of pig breeding organizations is decreasing. This results in a small number of pig breeding organizations providing pigs to farms around the world in different environments (Knap, 2005). Modern pigs need to be capable of facing a range of environmental challenges, under the assumption that current regional swine housing persists for commercial herds. Elevated temperature limit pig reproduction (Nardone et al., 2006) and becomes increasingly important as pig production is moving to warm climates (FAO, 2006) and because of climate change (Hoffmann, 2010).

To assess the opportunities to add breeding for improved PFSP to the existing genetic selection for reproduction traits, parameters estimated included 1) genetic variation for PFSP and its component traits, 2) genetic correlations between PFSP, its component traits and sow reproduction traits, 3) genetic correlation between PFSP in temperate and heat challenged conditions.

5.2 Material and methods

Animal Care and Use Committee approval was not needed for this study because it utilized regularly collected data from the TOPIGS breeding program (Vught, The Netherlands). The TOPIGS breeding program operates according to the EFABAR code of conduct (Neeteson et al., 2006).

Data

Data were sourced from farms in Spain and Portugal that were breeding purebred Dutch dam line sows. The purebred Dutch line is a Yorkshire dam line and part of the TOPIGS breeding program (Vught, the Netherlands). Historically, selection in the Dutch line was operated by a large number of independent Dutch herd book multipliers which produced their own replacements. All farms were linked through a central database, common breeding goal and exchange of genetic material through use of approved AI boars. The breeding goal included litter size, litter mortality, daily gain, and back fat. The relative weights of the traits changed over time. Since 2000, farms in Spain and Portugal were added to the breeding program of this dam line. These farms were populated by importation of gilts from the Netherlands, included in the central database and used semen from approved AI boars.

For the current study lifetime reproductive performance data were available on 4,475 gilts from 17 Spanish and Portuguese farms which had their first insemination between January 2002 and January 2009 and were culled before December 2011. Fifty-nine sows were still alive in 2012 and as focus was on lifetime reproductive performance these sows were removed from the dataset. Sows were defined to change parity after weaning. Therefore, parity 1 runs from first insemination of a sow until the end of its first lactation, this also referred to as gilt. Parity 2 is a sow which weaned its first litter, parity 3 is a sow which weaned its second litter and so on. After editing, these data consisted of 22,759 insemination records from 4,398 sows from time of first insemination in its life until culling, from January 2002 until December 2011. Each parity record included sow identification number, birth date of the sow, parity, farm, date of first insemination in that specific parity, weaning to first insemination interval, date of successful insemination, service sire of first insemination, service sire of successful insemination, farrowing date, gestation length, non-return rate, farrowing rate, total born, number of piglets born alive, number of stillborn piglets, and weaning date. Additionally, age at first insemination and culling date were available for all sows. Full pedigree traced back 8 generations and contained 6,738 animals.

Trait definition

In-heat was defined as a binary trait for sows (parity >= 2) based on the interval from weaning to subsequent first insemination within a parity. In normal circumstances sows return to oestrus within a week after weaning (Ten Napel et al., 1995). Therefore in-heat was defined as 1 if weaning to first insemination interval was <= 7 days, and 0 if weaning to first insemination interval was longer than 7 days. For sows culled after weaning, in-heat was considered as missing value. Non-return rate was defined as a binary trait: 1 if the sow was not inseminated again within 28 days after first insemination and 0 if the sow had an additional insemination within 28 days after first insemination. For sows culled within 28 days after first insemination because of reproductive failure non-return rate was recorded as 0. For sows culled for other reasons, such as leg problems, within 28 days after first insemination non-return rate was considered as missing. Farrowing rate was defined as a binary trait: 1 if the first insemination resulted in a gestation length longer than 108 days, or if litter size from first insemination was at least 1 piglet. Otherwise farrowing rate was considered as 0. For sows culled after first insemination because of reproductive failure, farrowing rate was recorded as 0. For sows culled for other reasons after first insemination, such as leg problems, farrowing rate was missing. Number of piglets born alive and number of stillborn piglets was recorded within 24 hours of farrowing. Total born was then defined as the sum of number of piglets born alive and number of stillborn piglets. Total born ranged from 1 to 30. Prenatal survival rate (%) was defined as: ((number piglets born alive)(total born)$^{-1}$)*100. Selected for next parity was defined as a binary trait: 1 if the sow had an insemination in the next parity and 0 if the sow was culled within the current parity or after weaning.

Problem free sow production (**PFSP**) was defined as piglet production resulting from first insemination within a parity and being able to produce another parity. Problem free sow production in a parity was 1 when in that specific parity the following four criteria were met:

1. In-heat was 1 or parity was 1
2. Non-return rate was 1
3. Farrowing rate was 1
4. Selected for next parity was 1

Problem free sow production was 0 when 1 or more of the above criteria was not met (Figure 5.1).

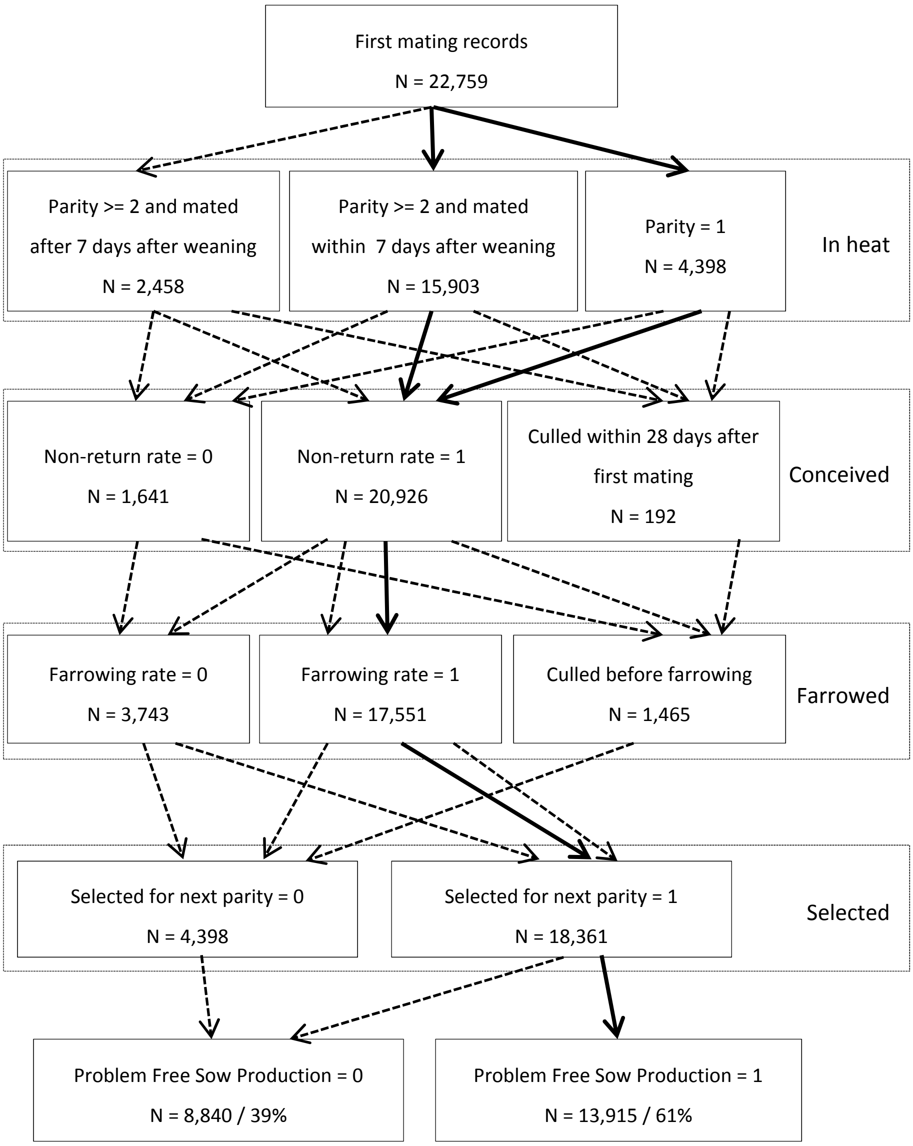

Figure 5.1 Flow-chart of problem free sow production in sows and numbers of observations for each trait. Black lines show the flow for problem free sow production within one parity, dotted line shows all other possible flows within a parity.

Meteorological observations

To be able to calculate heat load indices meteorological data were available from the European Climate Assessment Dataset (Klein Tank et al., 2002) and included daily summaries for the maximum, minimum and average outside temperature for 6 Spanish and 3 Portuguese weather stations and were available from January 2002 until June 2011. The closest available weather station was assigned to each farm. Most of the farms had a weather station within 122 km radius of the farm, with the closest being 45 km and the farthest being 209 km. These data were assumed to represent the temperature at these farms, as sows were housed in automatically controlled natural ventilated sheds (using wind breaking curtains), without any cooling. Freitas et al. (2006) estimated a correlation of 0.9 between on-farm temperature and weather station temperature in the US, even for weather stations more than 300 km from the farm.

Definition of heat load

A previous study (Bloemhof et al., 2008) revealed that reproductive performance of a sow remained fairly constant over a range of low and medium temperatures but decreased above an upper critical temperature (UCT). The UCT above which farrowing rate linearly decreased was estimated to be 19.2°C (Bloemhof et al., 2008). At day 21 prior to first insemination heat stress had the largest effect on farrowing rate (Bloemhof et al., 2013). In the current study, the heat load index for PFSP in-heat, non-return rate, farrowing rate, and selected for next parity was defined as the deviation of the maximum temperature from 19.2°C at day 21 prior to first insemination. Below 19.2°C the heat load index for PFSP, in-heat, non-return rate, farrowing rate, and selected for next parity was set to 0.

Heat stress on day of insemination had the largest effect on total born (Bloemhof et al., 2013). The UCT above which total born linearly decreased was estimated to be 21.7°C (Bloemhof et al., 2008). According to this, the heat load index for total born, number born alive, number stillborn, and prenatal survival rate was defined as the deviation from 21.7°C of the maximum temperature at day of insemination. Below 21.7°C the heat load index for total born, number born alive, number stillborn, and prenatal survival rate was set to 0.

Descriptive statistics

Descriptive analysis of the data was performed using the MEANS procedure (SAS Inst. Inc., Cary, NC). To determine if there were differences in reproductive performance in temperate and heat challenged conditions, the observations were divided in observations in temperate and heat challenged conditions based on the heat load index. If the heat load index for PFSP was larger than 0 the observation was assigned to heat challenged conditions. If the heat load index for PFSP was 0, the observation was assigned to temperate conditions. Differences in means between temperate and heat challenged conditions were tested for significance using the TTEST procedure in SAS 9.2 (SAS Inst. Inc., Cary, NC).

Estimation of variance components

Variance components for traits related to easy to manage sow productivity, the compound trait called PFSP and traits related to sow reproduction were estimated using Gibbs sampling based on an animal model. A repeatability model was used for all traits except for selected for next parity. The general formulation of these animal models in matrix notation is:

$$y = Xb + Za + Wc + Fm + Us + e \qquad [1]$$

where y is a vector of unobserved liabilities to the binary traits and for the continuous traits a vector of observations, *b* is a vector of fixed effects; *a* is a vector of the random animal genetic effect; *c* is a vector of the random permanent non-genetic animal effect; *m* is a vector of the random farm-year-month effect; *s* is a vector of the random service sire effect, *e* is a vector of the random residual effect, and X, Z, W, F, and U are the respective incidence matrices. Variances were:

$$Var\begin{bmatrix} a \\ pe \\ fym \\ ss \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & 0 & 0 & 0 & 0 \\ 0 & \mathbf{I}_{pe}\sigma_{pe}^2 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}_{fym}\sigma_{fym}^2 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{I}_{ss}\sigma_{ss}^2 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}_e\sigma_e^2 \end{bmatrix}$$

where **A** is the additive relationship matrix, $\mathbf{I}_{pe}$, $\mathbf{I}_{fym}$, $\mathbf{I}_{ss}$, $\mathbf{I}_{e}$ are identity matrices and $\sigma_a^2, \sigma_{pe}^2, \sigma_{fym}^2, \sigma_{ss}^2, \sigma_e^2$ are animal, permanent environmental, farm-year-month, service sire, and residual variances, respectively. The fixed and random effects included for each trait are given in Table 5.1.

Table 5.1 Fixed effects, covariables and random effects included in the genetic models for problem free sow production (PFSP), in-heat (IH), non-return rate (NR), farrowing rate (FR), selected for next parity (IS), age first insemination (AFI), prenatal survival rate (PSR), total born (TB), number born alive (NBA), and number stillborn (NSB).

	Fixed effects[1]			Covariables[2]			Random effects[3]				
	parity	re-breeding	pb/cb	lac.length	hl day ins	hl day -21	animal	pe	fym-ins	fym-farr	ss
PFSP	×					×	×	×	×		×
IH	×			×		×	×	×	×		
NR	×					×	×	×	×		×
FR	×					×	×	×	×		×
IS	×					×	×		×		
PSR	×	×	×		×		×	×		×	×
TB	×	×	×		×		×	×		×	×
NBA	×	×	×		×		×	×		×	×
NSB	×	×	×		×		×	×		×	×

[1] parity = parity of the sow, parity 8 and higher were combined resulting in eight classes; re-breeding= farrowed from first or later insemination, two classes; pb/cb= litter purebred or crossbred, 2 classes.

[2] lac.length = length of previous lactation in days; hl day ins= heat load at day of insemination in ˚C; hl day -21 = heat load at 21 days before first insemination in ˚C.

[3] animal = genetic animal effect; pe= permanent non-genetic animal effect; fym-ins= farm-year-month of insemination effect; fym-farr= farm-year-month of farrowing effect; ss= service sire effect.

Heritability and repeatability for PFSP, its underlying components and reproduction traits were estimated in a univariate analyses. A multi-trait analysis was run incorporating all studied traits to estimate genetic correlations. In these analyses the animal and permanent environmental effects were assumed to be correlated between traits and all remaining covariances were assumed to be zero.

Variance component estimates of PFSP in temperate and heat challenged conditions

To determine the relationship between PFSP in temperate and heat challenged conditions, observations were divided in observations with and without heat challenges based on the heat load index. If the heat load index for PFSP was larger than 0 the observation was assigned to heat challenged conditions. If the heat load index for PFSP was 0, the observation was assigned to temperate conditions. Models for the analyses were as mentioned for model 1 except that the covariate heat load index was not included.

Gibbs samples settings

Variance components for the binary traits were estimated using a Bayesian threshold model via Gibbs sampling (THRGIBBS1F90-software; Tsuruta and Misztal, 2006). The THRGIBBS1F90 program is based on a probit model in MCMC setting (Sorensen and Ganiola, 2002). All parameter estimates for the binary traits were on a liability scale. Variance components for the linear traits were estimated via Gibbs sampling (GIBBS1F90- software; Misztal et al., 2002). Every tenth sample was saved to calculate posterior means and standard errors of variance components, heritabilities, and correlations. Convergence was visualized by plotting of Gibbs samples. The first 100,000 samples were removed as burn-in, and a total of 250,000-400,000 samples were used for the final computations.

5.3 Results

Problem free sow production

Problem free sow production (**PFSP**) is a trait combining several events within a specific parity. The flow of events resulting in a PFSP of 1 is shown in Figure 5.1. Only 61% of the first matings within a parity resulted in a PFSP of 1. Table 5.2 shows the descriptive statistics of the used dataset. From the inseminated sows 19% were culled and not used for an additional parity. On average in-heat was 0.87 indicating that 87% of the sows were inseminated within 7 days post weaning. Average non-return rate was 0.93 indicating that of those sows inseminated 93% of the sows conceived and maintained pregnancy until 28 days after first mating.

Average farrowing rate was 0.82 implying that from the first inseminations within a parity 82% resulted in a litter with at least a single piglet. Average total born per litter was 11.9 (± 2.8) piglets with on average approximately a single stillborn piglet per litter (Table 5.2). Difference in trait means between temperate and heat challenged conditions were tested for significance and are shown in Table 5.2. In heat challenged conditions PFSP was 0.08 lower ($P < 0.01$) than in temperate conditions. Sows experience more difficulties in returning to estrus after weaning when temperatures are high than under lower temperatures, as the trait in-heat was 0.05 lower ($P < 0.01$) in heat challenged conditions. In heat challenged conditions farrowing rate was 0.79 indicating that 79% of the first inseminations within a parity resulted in a farrowing. Under non-challenged conditions farrowing rate was 0.86 indicating that under non-challenged conditions 86% of the first inseminations within a parity resulted in a farrowing ($P < 0.01$). No effect of temperature was found on the trait selected for next parity ($P = 0.15$). There was no effect of heat on total born ($P = 0.15$) suggesting the sow has the genetic potential to gestate a full litter regardless of external heat load. However, the number of stillborn piglets increased slightly ($P < 0.01$) under heat challenged conditions resulting in a 1% lower prenatal survival rate in heat challenged conditions than in temperate conditions. So while the genetic potential resulted in a piglet being born the heat load resulted in this piglet not being viable.

Table 5.2 Descriptive statistics of the overall dataset, in conditions under temperate and heat challenged conditions. The difference between temperate and heat challenged conditions was tested for significance using a T-test and the P-value is shown.

	Overall			Temperate			Heat			Temperate vs. heat	
Trait:	N	mean	SD	N	mean	SD	n	mean	SD	difference	P-value
Problem free sow production	22,759	0.61	0.49	10,363	0.65	0.48	12,023	0.57	0.49	0.08	<0.01
In-heat	18,361	0.87	0.34	8,235	0.89	0.31	9,835	0.84	0.36	0.05	<0.01
Non-return rate	22,567	0.93	0.26	10,300	0.93	0.25	11,899	0.92	0.27	0.01	<0.01
Farrowing rate	21,294	0.82	0.38	9,787	0.86	0.35	11,161	0.79	0.40	0.07	<0.01
Selected for next parity	22,759	0.81	0.40	10,363	0.81	0.39	12,023	0.80	0.40	0.01	0.15
Prenatal survival rate	20,538	92.1	13.8	9,503	0.93	0.13	10,704	0.92	0.14	0.01	<0.01
Total born	20,538	11.90	2.80	9,503	11.92	2.71	10,704	11.86	2.87	0.06	0.12
Number born alive	20,538	10.92	2.83	9,503	10.99	2.75	10,704	10.86	2.88	0.14	<0.01
Number still born	20,538	0.98	1.68	9,503	0.93	1.64	10,704	1.01	1.69	-0.07	<0.01

Variance component estimates of PFSP, the component traits and general sow reproduction traits

Heritability estimates for the binary traits (Table 5.3) were highest for in-heat (0.18 ± 0.02) and lowest for selected for next parity (0.04 ± 0.01). Problem free sow production had a heritability estimate of 0.06 ± 0.01. Genetic variances ranged from 0.05 ± 0.01 for selected for next parity up to 0.30 ± 0.04 for in-heat. Permanent environmental variances for PFSP, FR, and NR were as large as their genetic variances. However, for in-heat permanent environmental variance was almost 4 times smaller than its genetic variance. Farm-year-month variances for PFSP, in-heat, and farrowing rate were as large as their genetic animal variances. Farm-year-month variance for non-return rate was only half of the genetic animal variance. However, farm-year-month variance for selected for next parity was 5 times larger than its genetic variance. Service-sire variances were small for PFSP, non-return rate and farrowing rate.

Heritability estimates for the reproduction traits (Table 5.3) were highest for total born (0.10 ± 0.01) and lowest for prenatal survival rate (0.04 ± 0.01). Within total born, number stillborn and number born alive, genetic variances and permanent environmental variances were almost similar in size. For prenatal survival rate permanent environmental variance was almost twice as large as the genetic variance. Farm-year-month of farrowing variance was smaller than their genetic variance for all four reproduction traits. Service-sire variance was small for all traits.

Table 5.3 Estimated heritabilities and variance components with corresponding SE (in parentheses) for problem free sow production (PFSP), in-heat (IH), non-return rate (NR), farrowing rate (FR), selected for next parity (IS), prenatal survival rate (PSR), total born (TB), number born alive (NBA), and number stillborn (NSB).

	Parameter[1]							
Trait:	h^2	σ_a^2	σ_{pe}^2	$\sigma_{fym-ins}^2$	$\sigma_{fym-farr}^2$	σ_{ss}^2	σ_e^2	σ_p^2
PFSP	0.06(0.01)	0.08(0.01)	0.06(0.01)	0.10(0.01)	-	0.04(0.01)	1.00(0.01)[2]	1.28(0.02)
IH	0.18(0.02)	0.30(0.04)	0.08(0.03)	0.29(0.03)	-	-	1.00(0.02)[2]	1.67(0.02)
NR	0.06(0.02)	0.08(0.02)	0.07(0.03)	0.04(0.01)	-	0.02(0.01)	1.00(0.01)[2]	1.21(0.03)
FR	0.08(0.02)	0.10(0.02)	0.08(0.02)	0.10(0.02)	-	0.02(0.01)	1.00(0.01)[2]	1.30(0.03)
IS	0.04(0.01)	0.05(0.01)	-	0.24(0.02)	-	-	1.00(0.01)[2]	1.29(0.03)
Reproduction:								
PSR	0.04(0.01)	8.13(1.93)	14.11(1.86)	-	6.95(0.86)	1.49(0.45)	154.19(1.77)	184.87(2.06)
TB	0.10(0.01)	0.78(0.12)	0.77(0.08)	-	0.55(0.06)	0.08(0.02)	5.37(0.06)	7.55(0.10)
NBA	0.08(0.01)	0.61(0.10)	0.85(0.08)	-	0.27(0.04)	0.09(0.02)	5.88(0.07)	7.71(0.09)
NSB	0.06(0.01)	0.17(0.03)	0.19(0.03)	-	0.20(0.02)	0.02(0.01)	2.22(0.03)	2.80(0.03)

[1] h^2= heritability, σ_a^2**=** genetic variance, σ_{pe}^2= permanent environmental variance, $\sigma_{fym-ins}^2$= farm year month of insemination variance, $\sigma_{fym-farr}^2$= farm year month of farrowing variance, σ_{ss}^2= service sire variance, σ_e^2= residual variance, σ_p^2= phenotypic variance.

[2] residual variance is 1.00 by definition

Genetic correlations between PFSP, the component traits, and general sow reproduction traits

Genetic correlations between PFSP and its component traits are shown in Table 5.4. Strongest genetic correlation was estimated between PFSP and farrowing rate (0.82 ± 0.05), followed by the genetic correlation between PFSP and in-heat (0.75 ± 0.06), and between PFSP and non-return rate (0.69 ± 0.08). The smallest, although still moderate, genetic correlation was estimated between PFSP and selected for next parity (0.46 ± 0.24), and this estimate also showed the largest standard error. Genetic correlations between the component traits ranged from 0.07 ± 0.27 between farrowing rate and selected for next parity up to 0.96 ± 0.02 between non-return rate and farrowing rate. The latter correlation implies that non-return rate and farrowing rate are genetically the same trait.

Genetic correlations between PFSP and sow reproduction traits are shown in Table 5.5 and ranged from -0.18 ± 0.12 between PFSP and number still born to 0.28 ± 0.12 between PFSP and prenatal survival rate.

Table 5.4 Genetic correlations with corresponding SE (in parentheses) between problem free sow production (PFSP), in-heat (IH), non-return rate (NR), farrowing rate (FR), and selected for next parity (IS).

Trait:	PFSP	IH	NR	FR
IH	0.75(0.06)			
NR	0.69(0.08)	0.08(0.13)		
FR	0.82(0.05)	0.27(0.11)	0.96(0.02)	
IS	0.46(0.24)	0.60(0.22)	0.08(0.28)	0.07(0.27)

Table 5.5 Genetic correlations with corresponding SE (in parentheses) between problem free sow production (PFSP), and prenatal survival rate (PSR), total born (TB), number born alive (NBA), and number stillborn (NSB).

Trait:	PFSP
PSR	0.28(0.12)
TB	0.14(0.12)
NBA	0.26(0.13)
NSB	-0.18(0.12)

Variance component estimates of PFSP in temperate and heat challenged conditions

Variance component estimates of PFSP in temperate and heat challenged conditions are shown in Table 5.6. Heritability of PFSP in heat challenged conditions was 3% higher than heritability of PFSP in temperate conditions (0.08 ± 0.01 and 0.05 ± 0.01, respectively). Genetic variance in heat challenged conditions was twice as large as the genetic variance of PFSP in temperate conditions (0.12 ± 0.02 vs 0.06 ± 0.02). Genetic correlation between PFSP in temperate and heat challenged conditions was estimated to be not significantly different from unity (0.93 ± 0.07). Permanent environmental variance in heat challenged conditions was 0.09 ± 0.02 compared to 0.05 ± 0.02 in temperate conditions. Farm-year month variance in heat challenged conditions was 0.25 ± 0.02 whereas farm-year-month variance in temperate conditions was only 0.10 ± 0.02. Service sire and residual variance did not differ between the 2 environmental conditions. As a result phenotypic variance in heat challenged conditions was 1.51 ± 0.05 which is 20% larger than phenotypic variance in temperate conditions (1.25 ± 0.03).

Table 5.6 Estimated heritabilities, variance components and genetic correlations with corresponding SE (in parentheses) for problem free sow production (PFSP) in temperate and heat challenged conditions.

		PFSP	
Parameter	Definition	Temperate	Heat challenged
h^2	Heritability	0.05(0.01)	0.08(0.01)
r_g	Genetic correlation	0.93(0.07)	
σ_a^2	Genetic variance	0.06(0.02)	0.12(0.02)
σ_a	Genetic covariance	0.08(0.02)	
σ_{pe}^2	Permanent environmental variance	0.05(0.02)	0.09(0.02)
σ_{pe}	Permanent environmental covariance	0.06(0.02)	
σ_{fym}^2	Farm-year-month of insemination variance	0.10(0.02)	0.25(0.02)
σ_{ss}^2	Service sire variance	0.04(0.01)	0.04(0.01)
σ_e^2	Residual variance[1]	1.00(0.01)	1.00(0.01)
σ_p^2	Phenotypic variance	1.25(0.03)	1.51(0.05)

[1] residual variance is 1.00 by definition

5.4 Discussion

Problem free sow production (**PFSP**) is a trait which can be improved via genetic selection which will result in a reduction of non-productive sow days at the herd level. Genetic correlations between PFSP and general sow reproduction were close to zero, implying that PFSP and sow reproduction can be simultaneously improved via genetic selection.

Problem free sow production

Pork supply chain productivity depends on several factors including production efficiency (feed efficiency, mortality, sow productivity), system throughput and carcass or product quality. Sow productivity depends on kilograms of pork produced per sow per year, and length of productive life. To improve sow reproductive performance (a component of kilograms of pork per year) we proposed here a new trait called PFSP at parity level, which incorporated the traits in-heat, non-return rate, farrowing rate, and selected for next parity. The sow performance level as shown in Table 5.2 is in line with general sow performance as described for Canada, USA, and the Netherlands (PigChamp, 2011a; PigChamp 2011b; Benchmark Agrovision, 2012).

As globally average herd size is increasing and amount of labour per sow is decreasing (Eurostat, 2010), sows require easy management. However, average level of PFSP in the current study was only 61%, which indicates that on average 4 out of 10 sows are not able to be problem-free within a parity. This results in additional farmer interventions whilst the additional labor might not be available.

Most sows are culled in lower parities because of reproductive failure (Engblom et al., 2007). However when estimating genetic parameters for reproductive performance traits, the culled sows are not included as these sows have no record for the reproduction trait and when one would include these records this gives noise to the genetic parameter estimate. The proposed trait PFSP includes in addition to the traits in-heat, non-return rate, farrowing rate also selected for next cycle. Genetic selection on improved PFSP will therefore lead potentially to sows which live longer.

Genetics of problem free sow production

Heritability for PFSP was low (0.06 ± 0.01), and this was in line with most female reproduction traits which are, in general, characterized by low to moderate heritabilities (Bidanel, 2011). Random permanent non genetic animal variance, farm-year-month variance and service sire variances for PFSP were substantial implying that large part of the variation in PFSP is due to environmental factors such as gilt rearing, AI-management, estrus monitoring, feeding, health of the farm, and season. In addition to optimization of management factors genetic selection on PFSP could result in a gradual permanent improvement of PFSP in the swine herd. To be able to calculate how much genetic improvement can be achieved within 1 generation, we estimated genetic variance for PFSP using a linear model, the estimated genetic variance was estimated to be 0.008. In general when applying single trait selection, one can improve one standard deviation per generation. Within the population under study with an average PFSP of 0.61, for one generation single trait selection PFSP can be improved by 0.09. This implies that within this population, given current management standards, after one generation of selection average PFSP will be improved to 0.70. This shows that improving PFSP through genetic selection can be reasonably successful. Although in reality single trait selection would not be utilized in a breeding program and PFSP would be considered as part of a wider selection index.

Highest heritabilities for female reproduction traits are generally found in traits depending solely on the sow’s genotype and not on that of her piglets, such as age at puberty and weaning to estrus interval (Bidanel, 2011). Highest heritability estimate obtained here was for the trait in-heat (0.18 ± 0.02), which is a trait which is solely depending on the genotype of the sow. Non-return rate and farrowing rate had heritabilities of 0.06 ± 0.02 and 0.08 ± 0.02, respectively which is in line with the heritability estimate of 0.06 for farrowing rate estimated in an earlier study (Bloemhof et al., 2012). Heritability estimates for total born, number born alive and prenatal survival rate were in line with those reported in literature (Bidanel, 2011).

Sow longevity is of interest for the pig industry both from an ethical and an economical point of view (Serenius and Stalder, 2006). Most authors study sow longevity by analyzing length of productive life or stayability up to a certain parity (Engblom et al., 2009). Disadvantage of this approach is that one needs to wait for the sow to be culled before one can analyze the trait. In the current study a trait called selected for next parity was defined, which indicates if a sow was inseminated in the parity after the current and which is therefore available on parity level. Heritability of this trait was 0.04 ± 0.01, which is comparable to heritability estimates for length of productive life (Serenius and Stalder, 2004; Engblom et al., 2009; Lewis and Bunter, 2011b).

Alternatives for problem free sow production

Selection for improved PFSP could result in a decreased number of non-productive sow days and an increased number of litters per sow per year at the herd level. Non-productive sow days are days that a sow is neither gestating or lactating

(Wilson et al., 1986) and are of significant cost to production systems. Including feed and piglet production losses, a Dutch study estimated the cost of one non-productive sow day to be €2.20 in the Netherlands (Wageningen Livestock Research, 2011). In the US costs of a non-productive (or 'not in pig' day) sow day range from $1.60 up to $2.60 (Rix and Ketchem, 2009). Non-productive sow days occur between weaning and insemination but also include the lost days when the gestation of a sow is unsuccessful, the conception fails, the sow aborts, or when the sow is removed from the production system (Wilson et al., 1986). Reduction of these non-productive days will result in an improved number of litters per sow per year and therefore to an improved herd productivity and in more profit. Non-productive sow days are generally used for management purposes as a measurement on herd level (Koketsu, 2005). Even though costs of non-productive sow days are high and improving the trait genetically can therefore be highly profitable, no studies have been performed on the genetic improvement of non-productive sow days at individual sow level. Improvement of PFSP via genetic selection has the potential to be highly profitable as it could reduce number of non-productive sow days.

Litters per sow per year are another indicator for sow productivity and incorporate traits like weaning to first service interval, farrowing rate, gestation length and lactation length. The trait litters per sow per year has shown to have a heritability of 0.03 in a population of Landrace and Large White sows (Abell et al., 2012). Disadvantage of selection on litters per sow per year is that to be able to calculate the trait a sows needs to remain in the sow herd for at least a year. However, in general 15-20% of the culled sows have only produced one litter (Engblom et al., 2007); these sows have not been able to express their full genetic potential for the trait litters per sow per year. Problem free sow production can be calculated on parity level, using traits already available within management information systems, and will include all sows in the breeding herd which have been weaned at least once.

Implications for pig breeding

Genetic correlations between PFSP and its component traits were strong but below 0.9. Breeding for problem-free sows can therefore not be achieved by just selection on one of its component traits and could either be done by selection on all four component traits or by selection on the overall trait PFSP. Genetic evaluations within pig breeding nowadays involve a large number of traits (Dekkers et al., 2011); and including more traits could be computational demanding. Inclusion of a combined trait into the genetic evaluation is therefore preferred rather than adding four additional traits.

The genetic correlation between non-return rate and farrowing rate was 0.96 ±0.02 which implies that these traits are genetically identical. According to our results, sows which are genetically more likely to be inseminated within 7 days after weaning do not necessarily farrow from that first insemination as genetic correlation between in-heat and non-return rate and farrowing rate was low (0.08 ± 0.13 and 0.27 ± 0.11, respectively). However, Hanenberg et al. (2001) estimated a low negative correlation and Holm et al. (2005) estimated a strong positive correlation (0.7) between interval weaning to first insemination interval and farrowing rate. Therefore the genetic relation between in-heat and farrowing rate needs some more research.

Genetic correlation between PFSP and litter size was 0.14 ± 0.12, which implies that current selection strategies on litter size will not reduce or improve level of PFSP. As the genetic correlation between PFSP and prenatal survival rate was moderately positive, sows which are more problem-free have less stillborn piglets. Prenatal survival rate and PFSP can both be considered to be robustness traits. Knap (2005) described robustness of farm animals as ‘the ability to combine a high production potential with resilience to environmental stressors allowing unproblematic production’. Sows with high PFSP are having unproblematic production and are therefore robust animals.

The current study focused on the genetic relationship between PFSP and reproductive performance traits. The genetic relation between PFSP and finisher characteristics wasn’t studied. As profitability of the pork supply chain depends largely on market pig performance, such as feed efficiency, carcass quality and mortality, one should study the genetic relation between finisher characteristics and PFSP before inclusion of PFSP in a pig breeding program. This is critical as a dam line is 50% of the genetics of any commercial finisher animal.

Problem free sow production under heat challenged conditions

Heritability estimates and genetic variance of PFSP was larger in heat challenged conditions than in temperate conditions (0.08 ± 0.01 and 0.05 ± 0.01, respectively). Heritability and genetic variance of a trait are known to be sensitive to environmental factors (Hoffmann and Merilä, 1999). Increased additive genetic variances under heat challenged conditions have been found for growth in finisher pigs, non-return rate and milk production in dairy cows and in milk production of sheep (Ravagnolo and Misztal, 2000 and 2002; Finocchiaro et al, 2005; Zumbach et al., 2008). Genetic correlation between PFSP in heat challenged and temperate conditions was not significantly different from unity (0.93 ± 0.07), which implies that PFSP can be considered the same trait in the two environments. This is in accordance with the estimates by Lewis and Bunter (2011a) who estimated high and positive genetic correlations between total born in different seasons in Australia. In addition to the genetic variances, all other variances inflated as well when estimated under heat challenged conditions. Farm-year-month variance was 2.5 times larger in the heat challenged conditions than in the temperate conditions. This increase in variance might imply that farming in heat challenged conditions is more variable due to the heat influencing biological processes than farming in non-heat, more temperate, conditions and therefore it is more complex to control PFSP and other traits that involve the physiology of the animal.

Selection for production traits often increases environmental sensitivity (Van der Waaij, 2004). In finisher pigs and dairy cattle negative genetic correlations have been estimated between production and heat tolerance (Zumbach et al., 2008; Aguilar et al., 2009), which implies that selection strategies for (re)production traits in moderate climates increase environmental sensitivity of animals. This is not supported by the results in the current study, as a highly favorable correlation between PFSP in heat challenged and temperate conditions was estimated. Genetic selection on PFSP in temperate climates will result in an improved PFSP in temperate as well as in hot climates within the population studied.

Conclusion

Genetic selection for PFSP is possible. Adding PFSP to current dam line breeding goals considering litter size, mortality and finisher efficiency, will reduce the number of non-productive sow days, potentially increase sow longevity and potentially result in more system profit.

5.5 Acknowledgements

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6

General discussion

6.1 Introduction

The aim of this thesis was to improve understanding of the genetic aspects of heat stress sensitivity, ease-of-management traits, and sow reproductive performance. Two dam lines were compared for their differences in heat stress tolerance as measured by differences in reproductive performance (Chapter 2). Then these dam lines and their reciprocal crosses were analyzed for their genetic potential for farrowing rate and heat tolerance (Chapter 3). Within Chapters 2 and 3 only heat stress on day of insemination was considered. In Chapter 4 the effect of heat stress during each day of the reproduction cycle on farrowing rate and total born was quantified. Finally, the genetics of a novel trait called problem free sow production for sow efficiency and productivity under temperate and heat challenged conditions was investigated (Chapter 5).

In this final discussion chapter, the implications of the research within the wider context of pig breeding will be discussed. The focus of this thesis was on heat stress sensitivity, but as heat stress is only one of the challenges pigs have to face in their life the discussion will broaden this to environmental sensitivity and adaptability of pigs to environmental challenges. To understand how adaptable pigs need to be in the future, the discussion starts with developments and projections for the global pork industry in the near to mid-term future. The discussion will then continue with a review of what the findings in this thesis imply for the adaptability of sows to environmental challenges. To finish, the thesis will discuss implications for pig breeding programs in the global pork industry and the possibilities for selection on genetic adaptability of sows.

6.2 Developments in the global pork industry

The global pork industry is rapidly changing. To understand how adaptable pigs need to be in the future, developments in the global pork industry need to be recognized and accounted for. In this section the developments in the global pork industry are described and the implications for the commercial production of pork are outlined.

6.2.1 Social drivers of the global pork industry

Recently developed / rapidly industrializing countries (such as China, Brazil, India, and Russia) are currently experiencing high growth within their economies. With such growth there is improved wealth which results in decreased child mortality and increased life expectancy (Unicef et al., 2010). Therefore, in addition to other reasons, the global human population is expected to grow from 7 billion people in 2010 up to 9 billion people in 2050 as shown in Figure 6.1 (FAO, 2009).

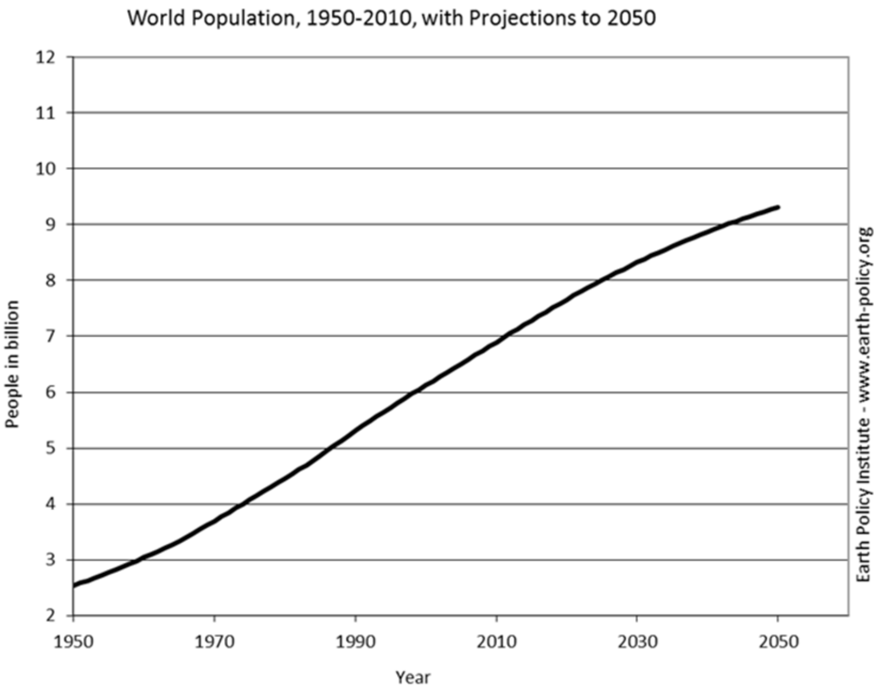

Figure 6.1 Growth of human world population as expected by FAO.

A major consequence of population growth is that all 9 billion people need to be fed. This is a huge challenge for the global food supply chain and the earth's natural resources. In addition to the growth of the human population improved wealth in areas with large populations (eg. Brazil and China) will result in a change in the average human diet. It has indeed been previously shown that when people have increased incomes one of the first things they do is change their diet (Jones, 2010). For example, in Mexico beans and tortillas are the main source of protein for the poorest people, whilst the people with higher incomes consume meat more regularly (chicken and pork). In general the more money available to a family the more meat and milk is consumed (Ghirotti, 1999). So at a basic level, both increasing population size and rising global wealth will result in an increased global meat demand.

Another effect of economic growth in developing economies is increased urbanization. It is expected that by 2050 67% of the human population will be living in cities vs. 52% in 2011 (UN, 2012). Urbanization leads to an increased consumption of fruit, vegetables, dairy, fish, and meat (Ghirotti, 1999; FAO, 2009). An example of this is China: in the past decade income has grown and as a result pork consumption per urban head has increased 21%, from 16.7 kg pork per head in 2000 up to 20.5 kg in 2009 (Xiao et al., 2012). As urbanized people tend to favour semi-processed or ready to eat foods, market chains for human food supply will move further towards concentrated supermarket chains (FAO, 2009). Even though the world’s urbanized population is growing and income is higher, the expectation is that in 2050 there will be still approximately 500 million people having problems in fulfilling their basic nutritional needs. This is a major concern not only from the hunger perspective but poverty and hunger can result in significant social disruptions and can even lead to war (Lagi et al., 2011) which can also have large negative effects on food production.

Food is currently mainly produced in rural areas. When countries become more industrial, people start to move into cities and the number of people working in agricultural industry in rural areas has been shown to decrease (FAO, 2009). This implies that agricultural productivity per rural head needs to increase and this leads to an increased reliance on commercial agriculture.

The challenge for agriculture to meet the increased meat demand is huge. However there is still some potential for increased meat production within developing countries. In developed countries, since the 1950’s, meat production has increased around 300%, largely due to increased animal efficiency through animal breeding, building of improved housing for the animals, optimization of diets and further improvement of herd management (OECD/FAO, 2012). The off-take ratio, which is the gross pork production of a country divided by the total pig inventory in that country, and realized and expected growth of this ratio is shown in Table 6.1 for different countries.

The off-take ratio is much higher in developed countries than in the developing countries. However, the expected growth in pork production per pig is much larger in the developing countries than in the developed countries. These data implies that animal efficiency in these countries can potentially increase by improving animal efficiency through improved herd management and nutrition in combination with the importation or improvement of animal genetics (OECD/FAO, 2012). However, even though there are still possibilities for further intensification of agriculture, it remains to be determined if this will be enough to meet the growing food demand.

Table 6.1 Off-take ratio, gross pork production of a country divided by the total pig inventory in that country, realized growth in off-take ratio in 1985-2011, and expected growth of off-take ratio in 2012-2021 for developing and developed countries, adapted from OECD/FAO, 2012[1].

Country:	Offtake ratio 2005-2009 kg/head	Realized growth 1985-2011 %/yr	Expected growth 2012-2021 %/yr
Developing countries[2]:			
Argentina	122	4.2	2.3
Brazil	83	5.3	3.2
China	108	3.0	1.7
Indonesia	93	1.4	0.8
Russia	122	3.2	2.0
South Africa	139	2.9	1.5
Thailand	108	1.4	0.7
Developed countries[2]:			
Australia	144	1.2	0.7
Canada	174	2.0	1.1
E27	144	1.0	0.7
Japan	130	-0.2	-0.1
United States	153	0.9	0.5
World	111	1.5	1.2

[1] http://dx.doi.org/10.1787/888932640084, accessed February 7 2013

[2] Definition of developing and developed countries is according to OECD (Organisation for Economic Co-operation and Development), http://www.oecd.org/

6.2.2 Pig feed availability

Through the increased meat demand in the world, the demand for the raw materials for production of pork will increase as well. Most pig diets today are grain / corn / soy based, therefore pig feed is competing with potential human food for energy and protein sources. As an example, in 2004 the total amount of human edible protein going into livestock feedstuffs was 77 million tonnes of protein a year. The total amount of human edible protein coming out of livestock was 58 million tonnes (FAO, 2006). This is mainly a result of the grain based diets fed to poultry and pigs, which have more similar nutritional requirements to human than diets fed to cows, sheep and goats have. This comparison does not take into account that animal protein has a higher nutritional value for humans than the human edible protein going into pig and poultry diets. But from this comparison it is evident that given the current diets fed to poultry and pigs, animal protein is not the most efficient protein source for feeding the world.

For the production of corn / soy / grain arable land is required. Since the 1850s many natural habitats have been converted to cropland or pastures (Goldewijk and Battjes, 1997). Between 1950 and 1980 the amount of arable land has expanded globally 100%, currently the global arable land expansion has slowed down (FAO, 2006). A major issue is that arable land size is naturally limited, whilst the food demand is still increasing. Intensification of crop yields per hectare is one way to meet the growing food demand. For instance, from 1989 to 2004 global cereal yield has increased 46% whilst the arable land growing cereals decreased 5% (FAO, 2006).

Another competing factor for human and pig feed availability is the production of bio-fuels (ethanol). Bio-fuel is produced from grain, soy, corn, or rice. Due to increased prices for crude oil, the bio-fuel demand, and bio-fuel production has gone up in recent years (FAO, 2009). This puts pressure on human food and pig feed availability. In 2008, 10 percent of the worlds' grain production was used for the production of bio-fuel. This percentage is expected to increase in the future (FAO, 2009). Bio-fuel production is therefore a major risk for human food and pig feed availability.

To mitigate the risk posed from bio-fuels livestock producers can utilize the natural adaptability of livestock species. For example pigs are omnivores and were historically used as waste converters by feeding them human food leftovers (Zijlstra and Beltranena, 2013). In the past 50 years advanced diet formulation has been a key component part of the recorded improved growth rates of commercial pigs. Whereas in the past human food leftovers were the primary diet these were replaced by high energy diets based on corn, soy and grain. But projecting into the future, with the current feed availability challenge, it will perhaps become beneficial again to use pigs as efficient converters of by-products into pork (Zijlstra and Beltranena, 2013). Within bio-fuel production processes a large amount of by-products and potentially ingredients for pig diets are produced. These distillers dried grains can be utilized in pig diets and will then be converted to pork and thus edible protein for the growing human population (Stein and Shurson, 2009). Additionally to byproducts of biofuel production, human food waste (swill) can be used as pig feed as well. Swill can be any type of product that is coming available during human food production, processing, transportation, distributing or consumption of food (Westendorf et al., 2004). Swill can replace grain in pig diets without compromising growth, which will give in addition a sustainable solution for upgrading food waste to pork (Myer et al., 1999; Márquez and Ramos, 2007). Using food waste as pig feed is not new as in the past human food leftovers were already fed to pigs. However, for safety and health reasons feeding swill to pigs has been banned by the European Union and several states in the United States (Myer et al., 1999; European Parliament, Council, 2002). The foot-and-mouth-disease outbreak in the UK in 2001 was caused by feeding contaminated swill (Anderson, 2002). However if swill has been heated, the risk of spreading disease can be eliminated (Haapapuro et al., 1997). Around 30 to 40% of the human food in the developed countries is lost to waste (Godfray et al., 2010) and this gives a huge potential for livestock feed. Therefore policy makers should reconsider the ban of feeding heat treated swill to livestock / pigs as this might solve part of the livestock feed availability challenge. Another alternative for replacement of proteins coming from grain / soy / corn in pig diets might be feeding of insects to pigs. Insects can be grown on bio-waste or compost and can turn this into protein. Using insects then as feeding ingredient for pig diets gives an opportunity for fulfilling the globally demand for protein. However, the application of feeding insects to pigs is something for the future (Wageningen UR Livestock Research, 2012).

6.2.3 Global warming

Large emission of greenhouse gases has led to global warming and climate change (Stavi and Lal, 2013). Industrialization (early 1900's) has resulted in large emissions of greenhouse gases with detrimental effects on global warming. Global warming will result in increasing temperatures, more extreme weather conditions, and rising sea levels (FAO, 2006). Since 1800's the average temperature on earth has increased 0.8°C, for the next century average temperature is expected to increase by 1.8°C to 4.0°C. The impact climate change will have on crop production is different for the Southern and Northern hemispheres (FAO, 2009). The expected increase of temperature in the Northern hemisphere will benefit the crop production as length of the growth season may become longer, crop yield might increase and arable crop land size might increase. On the other hand the Southern hemisphere is expected to suffer from the more extreme weather events such as flooding and droughts (FAO, 2009). However, even though the expected positive effect of climate change on agriculture in the Northern hemisphere, the net effect of climate change on crop production is expected to be negative.

While feeding the world is a major challenge for the livestock industry, an additional concern is the impact livestock production has on global warming. Of the total global greenhouse gas emission 18% is due to livestock production (FAO, 2006). Beef and milk production by ruminants is responsible for 60% of the total greenhouse gas emission by livestock and pork is responsible for 26% (Bellarby et al., 2013). Even though this is much lower than the contribution ruminants have, if pork can be produced more efficiently, the negative effects on the environment can be reduced. The carbon footprint of pork quantifies all greenhouse gases expelled during pork production and is mainly due to feed production, manure processing and energy usage in animal houses (FAO, 2006). A pig's feed conversion reflects the amount (kg) of feed needed to produce one kg of pork. If a pig has a lower feed conversion, the amount of feed needed to produce pork is lower. Utilizing genetic selection on feed conversion the carbon footprint due to pork production can be decreased. For example, genetic selection in the past 35 years has improved lean growth rate in pigs and as a result nitrogen excretion in pigs has been reduced by 25% per animal and by 31% per kilogram of protein produced (Neeteson-van Nieuwenhoven et al., 2013). If feed conversion of pigs can be reduced even further by efficient breeding and future management, environmental and nutritional developments, the amount of feed sources to produce one kg of pig meat can be further reduced.

6.2.4 Implications for future pork production

In this section trends were discussed that show an increased worldwide demand for pork whilst an increasing shortfall in available feed. Consequently, the environmental impact of the pork industry needs to be reduced and agricultural productivity per rural head needs to increase. All these developments imply that to be able feed the urbanized human population pork production efficiency needs to increase further and possibly faster (Neeteson-van Nieuwenhoven et al., 2013).

6.3 Adaptability of sows

As discussed in the previous section pork production should become more efficient, for example by increasing farm sizes. The current trend is already that pork production is moving towards more large-scale units (Sosnicki and Newman, 2010). This might result in increased infection pressure, larger group sizes and decreased amounts of available labour per pig. As described earlier in this chapter pig production is moving to warmer climates and feed quality is changing because of inclusion of by-products from bio-fuel production and potentially by feeding swill to pigs. Pigs are therefore facing quite different environments than what they have been selected for. Pigs of the future need to be able to produce well in these challenging conditions. Within this thesis the genetic aspects of heat stress sensitivity, and reproductive performance were studied. In this discussion heat stress sensitivity will be used as an example of adaptability of sows.

6.3.1 Performance and high temperatures

Pigs are sensitive to high temperatures. They cannot sweat and therefore need to regulate their body temperatures through increased respiration or panting. Pigs that suffer from heat stress also respond by increasing the blood flow to the skin to allow evaporation (Black et al., 1993). All these responses to high temperatures are less effective to cool down than sweating. It is the inability to cope with high temperatures that leads to heat stress. Wild pigs suffering from heat stress wallow in water or mud and change their 'normal' activities from day to night to regulate their body temperature (Bracke, 2011). In the modern pig industry pigs have to cope with heat stress within given environments, often without availability of water or mud. As a consequence of genetic selection for increased leanness, to improve efficiency, in the past 50 years internal heat production of pigs has increased (Brown-Brandl et al., 2004). Higher internal heat production lowers heat tolerance capacity, resulting in increased sensitivity to high temperatures (Brown-Brandl et al., 2001).

Heat stress of pigs is expressed in increased rectal temperatures, respiration rate, and skin temperature (Omtvedt et al., 1971; Black et al., 1993). Next to these physiological indicators of heat stress the effect of heat stress can also be measured in terms of reduced performance. High temperatures are known to negatively affect daily feed intake of sows, reproductive performance of sows, and finisher growth (Quiniou et al., 2001; Zumbach et al., 2008; Lewis and Bunter, 2011a; Bergsma and Hermesch, 2012). Reduced lactation feed intake will lead to increased body weight loss of the sows in lactation (Bergsma et al., 2008) resulting in a negative energy balance. A negative energy balance during lactation results in prolonged weaning to first service interval, reduced farrowing rate and reduced litter size in subsequent parities (Thaker and Bilkei, 2005) which can have major economic implications for the farm. High temperatures in the period around three weeks before insemination were identified in Chapter 4 as having the largest negative impact on the farrowing rate of sows. This period coincides with the lactation period of sows. The negative effect of temperature on farrowing rate of sows may therefore be due to a reduced lactation feed intake of sows resulting in reduced follicle development during and immediately after lactation (Quesnel et al., 1998). This impaired follicle development could explain the lower litter sizes and reduced farrowing rates in heat stressed sows.

6.3.2 Upper critical temperatures

Pig performance suffers from heat stress when ambient temperature exceeds the upper critical temperature of the pigs' thermo-neutral zone. This thermo-neutral zone is the range of temperatures between the lower and upper critical temperature (Bianca, 1976). Below the lower critical temperature of the thermo-neutral zone, a pig needs to increase heat production via shivering and other processes to maintain body temperature. Above the upper critical temperature of the thermo-neutral zone, the animal starts to be heat stressed and energy is used to get rid of excess heat through the lungs by increasing respiration rate (Black et al., 1993). In Chapter 2 a plateau-linear regression model was used to describe a thermo-neutral zone for farrowing rate and litter size of two dam lines. The upper critical temperature of this thermo-neutral zone was defined as the temperature above which farrowing rate and litter size started to decrease. The upper critical temperature for sows from the Dutch (D) line was estimated to be around 20°C, for International Large White (ILW) line sows no upper critical temperature could be estimated. The 20°C is numerically lower but in line with the upper critical temperature of 22°C which has been reported for lactating sows (Black et al., 1993).

6.3.3 Adaptation of sows to heat stress

The results in Chapter 2 showed that farrowing rate and litter size of D-line sows is at maximum level under temperate conditions and reduces in presence of heat stress. However, in Chapter 4 it was shown that within the D-line there are differences in response to high temperatures among different families. Farrowing rate and litter size of the ILW-line was not affected by temperature. An important remaining question is also whether there are physiological differences between sows that are able to keep producing under high temperatures and sows that need to reduce their performance under high temperatures. Understanding these differences would help in making selection decisions, although this was beyond the scope of this thesis. It has, however been shown that high temperatures lead to a reduction in feed intake of lactating sows (Black et al., 1993, Lewis and Bunter, 2011a; Bergsma and Hermesch, 2012) which may result in lower reproductive performance problems in subsequent parity. It can be hypothesized that the feed intake capacity of sows able to cope with high temperatures is higher than the feed intake capacity of sows which have problems with high temperatures. Unfortunately no feed intake records (gestation or lactation) were available for the sows used in this study.

6.3.4 Genetic differences between dam lines

When evaluating dam line breeding goals for the TOPIGS breeding program (Chapter 2) there were differences in appreciation between a Dutch Yorkshire dam-line and an International Large White line used by producers in Spain (warm climate) and the Netherlands (temperate climate). The Spanish producers preferred the ILW-line, whilst the Dutch producers preferred the D-line. When analyzing reproductive performance in relation to temperature for both of the dam-lines, no upper critical temperature could be estimated for reproductive performance of the ILW-sows (Chapter 2). The upper critical temperature of D-line sows, however, was estimated to be 19.2°C for farrowing rate and 21.7°C for litter size. Above these upper critical temperatures farrowing rate and litter size of D-line sows decreased linearly. For temperatures below 23°C farrowing rate, litter size, and piglets born from first insemination were highest for D-line sows. As a result above 24°C litter size was similar in both dam lines. However, farrowing rate and piglets born from first insemination were higher for the ILW-line sows compared to the D-line sows when temperature exceeded 25°C (Chapter 2).

6.3.5 Selection history

Large White and Yorkshire sows are in general similar breeds with similar levels of performance (Buchanan and Stalder, 2011). However, the International Large White dam line and the Dutch Yorkshire dam line studied in this thesis showed a clear difference in response to high temperatures. An explanation for this difference might be a difference in the selection strategies in these two dam lines. Both purebred lines, the D-line and the ILW-line, are part of the TOPIGS breeding program (Vught, the Netherlands). Historically, selection in the D-line was operated by a large number of independent Dutch herd book multipliers which produced their own replacements. All farms were linked through a central database, common breeding goal and exchange of genetic material through use of approved AI boars. The breeding goal included litter size, litter mortality, daily gain, and back fat. The relative weights of the traits used in the selection program changed over time. Since 2000, farms in Spain and Portugal were added to the breeding program of the D-line. These farms were populated by importation of gilts from the Netherlands, included in the central database and used semen from approved AI boars. The ILW-line sows were selected for more than 15 years based on data collected globally from multipliers located in a range of different environments (the Netherlands, Spain, Italy, the Phillipines, Brazil, South Africa etc). All these multipliers were linked through a central database and the breeding goal was similar to the breeding goal of the D-line. However, as selection in the ILW-line was based on data from not only temperate climates but also warm and tropical climates this has potentially favored families which have flatter reaction norms and thus had good reproductive performance in different climates. This may have resulted in an indirect selection on heat tolerance in ILW-sows and might explain why these sows have better reproductive performance under heat challenged conditions.

6.3.6 Genetic variation for heat tolerance

A way to improve environmental adaptability of pigs (e.g., breeding less heat sensitive pigs) is to explicitly define an all-encompassing adaptability trait that can be included into profit equations and that can be used in breeding goals. In Chapter 3 genetic variation was found for the random regression slope of farrowing rate against increasing temperature at day of insemination. This genetic variation was at 10 degrees above the upper critical temperature as large as the genetic variation for farrowing rate for D-line sows. The genetic variation estimated for the D-line was in line with other studies in which additive variances for heat tolerance were found to be important for fertility, production in dairy cattle, and growth in finisher pigs (Ravagnolo and Misztal, 2000 and 2002; Zumbach et al., 2008). It has been suggested that selection for production traits often increases environmental sensitivity (Van der Waaij, 2004). However, this was not supported by the genetic correlation between farrowing rate and the random regression slope which was estimated to be around 0 (Chapter 3). Additionally in Chapter 5 the genetic correlation between problem free sow production in non-heat stressed conditions (below 20°C) and in heat stress conditions (above 20°C) was estimated to be 0.93 ± 0.07, which implies that pigs with the best performance in a hot climate will also be the best in temperate climate too.

6.4 Implications for pig breeding

In the past decade consolidation in the global pig industry has led to large integrated pork production systems (integrators) which aim for increased production efficiency in the entire pork production chain (Sosnicki and Newman, 2010). Within this discussion it has been shown that pig industry is changing and the drivers for change are becoming ever more important. The findings of this thesis suggest that it is possible to breed pigs for improved adaptability to heat stress. This general discussion will finish with implications for pig breeding.

6.4.1 Aim of a breeding program

According to Dickerson and Hazel (1944) the first aim of a breeding program is to produce the most genetic improvement per time unit. Within each breeding program the breeding goal defines the goal of genetic improvement. The goal defines the production environment and which traits should be selected on for genetic improvement. The start of each breeding goal therefore should be first to investigate in which markets the product should be able to produce. If one knows which markets the product should produce the breeding structure can be defined. Therefore, breeding programs need to consider first for which market they want to produce pigs and adjust their breeding goal to be able to select for the requirements in that specific market(s).

6.4.2 Market

Globally operating pig breeding organizations are commercial companies. The primary goal of a commercial company is to make money and this is achieved when customers are profitable within their market. Customers of international pig breeding companies range from producers with large integrated systems in the USA, to high-input farms in northern Europe with environmentally controlled barns and high management, to low-input farms in parts of Asia that face health, climate and labour challenges. It has been postulated that these different customer types need different type of pigs due to genotype × environment interactions. The large integrated systems demand pigs which are efficient in growth rate and feed conversion, have low mortality and which are highly uniform and therefore can be managed in groups rather than as individuals. High-input farms in northern Europe with high management can manage pigs more individually to produce high quality meat, and often want the highest production per sow. Low-input farms which face large challenges demand robust and easy-to-manage pigs that produce with minimal inputs. Ideally a pig breeding company should supply these three markets with three different pig types assuming that any specific genotype is not sufficiently plastic to perform in two or even all three of these environments.

6.4.2 Breeding goal

If the target market is known then a specific breeding goal can be defined. Pig breeding programs are typically organized into a pyramid structure (Figure 6.2).

The genetic nucleus farm(s) at the top of the pyramid performs the actual breeding and selection of purebred animals. Therefore the genetic nucleus can be considered to be the engine of genetic improvement. The multiplication farms are responsible for the efficient multiplication of the purebred (elite) lines in a way as to not to dramatically increase genetic lag throughout the pyramid. Finally, at the commercial level the crossbreeding is performed to produce the F1 crossbred females. The F1 female is generally mated with a terminal boar (that can be pure or cross bred) to produce many efficient slaughter pigs. Even though selection decisions are made at the top of the pyramid in nucleus herds using purebred pigs, the breeding goal should be focused around enhanced commercial production (Figure 3) as this is where the revenue is generated in the system and performance is required / demanded by customers. The commercial success of a pig breeding program depends on delivering realized genetic progress (improvement) at the slaughter pig level and achieving product differential from competitor genetics. At a very basic level global pig farmers want many pigs which convert feed into meat efficiently, and have low mortality. In addition pigs should have the ability to efficiently produce in presence of commercial stressors (such as high temperature, diseases, etc.) and these basic principles equally apply globally regardless of climate or economic situation.

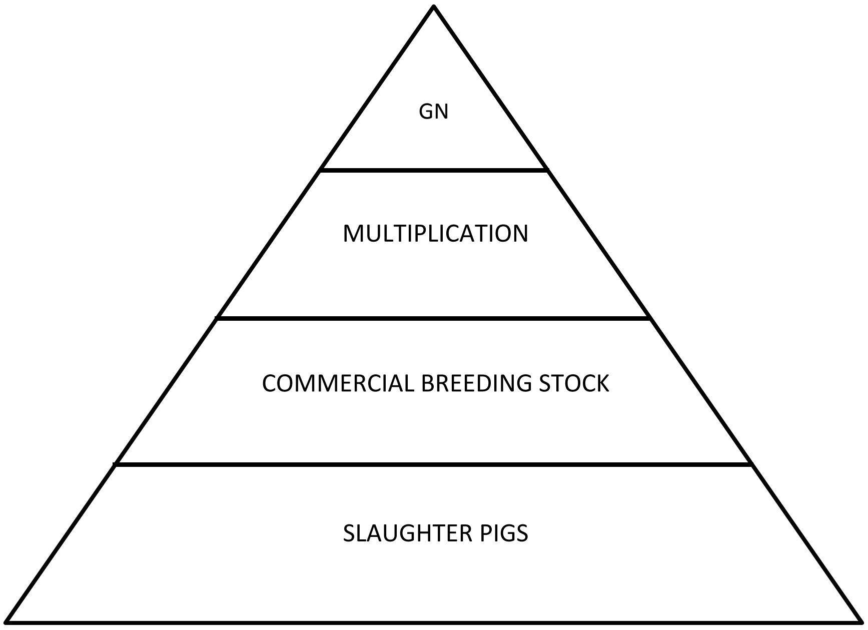

Figure 6.2 Pig breeding pyramid (GN = genetic nucleus).

6.4.3 Genetic selection

Traditionally nucleus farms operate under high management standards (e.g. controlled climate; disease free) (Knap, 2005). Genetic selection under optimal management standards has the potential to result in increased environmental sensitivity (Van der Waaij, 2004) if the information being used for the selection decisions also originates from systems with optimal management. Analogously, in Chapter 2 of this thesis D-line sows were found to be highly sensitive to increased temperatures where the phenotypic information used for selection over time all originated from a temperate climate. The phenomenon that selection on increased production results in increased environmental sensitivity has been identified in most livestock species such as broilers, pigs and dairy cattle (Rauw et al., 1998). Knap and Rauw (2009) argued that increased environmental sensitivity as a result of selection on high production level is caused by insufficient breeding goals as one could select on robustness directly or utilize information from multiple environments as to limit the effect of genotype × environment interactions during selection. As the D-line was selected on data collected in the Netherlands and their offspring needed to produce in Spain / Portugal, it may be obvious that these sows could potentially have production problems in Spain / Portugal. The data used in this thesis was collected from 2003 to 2011, gilts and sows were at that time housed in automatically controlled naturally ventilated barns (using curtains), without any mechanical cooling. As the daily temperatures are much higher in Spain/Portugal and management is different from that in the Netherlands this resulted in impaired performance as sows were genetically adapted to the Dutch conditions. Conversely, the ILW-line showed no negative response to elevated temperatures as they were selected based on data from multiple environments all around the globe. The example of the D-line and the ILW-line shows that selection needs to be done based on data collected in the environment where genetics is expected to produce. Therefore, international breeding companies need to account for the differences between selection and commercial production environments. Additionally in Chapter 3 a purebred-crossbred correlation between purebred and crossbred performance for farrowing rate was estimated to be < 0.6. A purebred-crossbred correlation < 0.8 implies that when selection is solely based on purebred performance this will result in a reduced selection response on crossbred level (Bijma and van Arendonk, 1998). Or in other words, the best purebreds do not breed the best crossbreds. To be able to select the right purebred animals on commercial performance a Combined Crossbred Purebred Selection strategy can be applied (Bijma and van Arendonk, 1998). In this strategy relatives of purebred animals are tested in commercial conditions, similar to progeny testing of international dairy bulls. The performance data from the relative's performance in commercial conditions and data from own performance in genetic nucleus conditions are combined in the genetic evaluation of the selection candidates. This results in selection of purebred animals which produce good crossbred offspring and perform well in commercial environments and are therefore more robust among environments.

6.4.4 Dilemma: Specialization or generalization

As described, pork is currently produced in a range of environments. If a breeding program focuses on genetic improvement across all these different environments, this may result in pigs that have best genetic potential across a wide range of environments, but that might not be the best product within each environment. So the long term danger for any specific breeding company is that if a competitor then focuses a product solely within one specific environment, the outcome from their genetics will be higher than that which was selected on performance in many different environments and thus the company with the more generic product would lose market share. Pig breeding organizations should therefore find a balance between costs of running different breeding programs (lines) and the number of markets they want to focus on.

6.5 Conclusion: where to go from here?

In this thesis it has been shown that it is possible to breed for improved heat stress resistance of sows in addition to improved production levels. However, it has also been shown that the genetic correlation between production in temperate climate and hot climate within a line is high. Given the range of temperatures included in this thesis, pigs within-line with the best performance in a hot climate will be the best in temperate climate too. Therefore in the context of a commercial breeding company with a crossbred evaluation program, breeding for improved heat stress resistance is not necessary. The most important issue for a pig breeding program is to define appropriate breeding goals which are based on the market pigs are expected to perform in and to include crossbred performance data in the selection of purebred pigs. Then data collection for genetic evaluation needs to be set up in that specific environment and this will favour pigs which are able to produce in that specific environment. This is expected to be a more powerful option than selecting for specific robustness, as it focuses on optimal production in different environments. This will result in unproblematic expression of production potential in a variety of environmental conditions.

It has previously been established that pig breeding organizations face a rapidly changing pork industry which results in larger herd sizes and more intensified systems. These more intensified systems will increasingly be provided by consolidated large producers and as a consequence even the associated industries i.e. building manufacturers operate on an international basis. The reduced number of major players in the pig industry will result in more standardized production environments on a global scale through the use of new technologies such as climate controlled barns. These trends are already firmly being established with the construction of modern swine production facilities in China and in Russia. To fulfill the needs of these major pork producers there will be increased consolidation in the breeding industry and this will be driven by product performance, product differentiation and implementation and execution of new technologies such as genomics. Considering the above social, economic, and scientific pressures it is the conclusion of this thesis that breeding for adaptability specifically will be of limited value in future breeding schemes. But this will be only the case when purebreds will be selected based on data from as well performance in the purebred herds as of data from relatives performing in commercial conditions. The largest challenge for pig breeding programs in the future will therefore be to individually identify and pedigree animals in commercial conditions.

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Summary

Summary

Globally the average size of pig herds are increasing and amount of labour spent per sow / finisher pig is decreasing. This requires sows which need less management intervention and which are easier to manage on a daily basis. In addition to easier manageable sows they will also need to be more adaptable considering that temperatures are expected to increase worldwide (1.8°C to 4.0°C in the next 90 years) and pork production is partially moving to warmer climates. The end result is that commercial pigs will potentially face more heat stress challenges during their productive life. During recent years the number of pig breeding programs has reduced and it is expected that by 2020 there will only be further consolidation. This leads to potentially (assuming the current diversity in pig rearing environments) a smaller number of pig breeding companies producing pigs for many different commercial environments. These environments differ in design, altitude, temperature, feed quality, health status and pig management. The objective of this thesis was to improve the understanding of the genetic aspects of heat stress sensitivity, ease-of-management traits, and sow reproductive performance.

Reproductive performance in dam lines is of great importance in commercial pig breeding programs. Heat stress has an adverse effect on reproduction. Pigs suffer from heat stress when temperature exceeds the upper critical temperature of the thermo-neutral zone. The thermo-neutral zone covers the range of temperatures between a lower and upper critical temperature. Above the upper critical temperature and below the lower critical temperature the pig needs to expend energy to maintain body temperature. In Chapter 2 differences in the relation between temperature and reproductive performance in two different dam lines were investigated and upper critical temperatures for reproductive performance of these two lines were determined. Data on farrowing rate, total born, and total born from first insemination was collected in Spain and Portugal from 2003 to 2005. Sows belonged to two purebred dam lines named Dutch (a Yorkshire dam line, originally selected in the Netherlands) and International (a Large White dam line, selected using global data). For each parity, the insemination records of the sows were used and combined with maximum outside temperature at day of insemination. The upper critical temperature for reproductive performance of Dutch line sows lies around 20°C. Above this temperature farrowing rate decreased with 1% per °C, total born decreased with 0.05 piglet per °C, and total born from first insemination decreased with 0.13 piglet per °C. Farrowing rate of the International line sows was not affected by temperature. Total born and total born

from first insemination of International line sows was adversely affected by temperature, however the adverse effect was less than in Dutch line sows. For temperatures below 23°C farrowing rate, total born, and total born from first insemination was higher for sows from the Dutch line than for sows from the International line. Above 24°C total born was almost the same in both dam lines, but when temperature exceeded 25°C farrowing rate and total born from first insemination were higher for the International line sows. The results shown in Chapter 2 imply that there are important differences in the relationship between temperature and reproductive performance traits in two genetically different dam lines, and these differences suggest that genetic selection on sow heat stress tolerance may be possible.

Building on the previous work, it was noted that fertilization and maintaining gestation in warm and hot climates is a challenge for sows. The pork supply chain values steady and undisturbed piglet production regardless of outside temperature. Farrowing rate can be defined as farrowing from first insemination within a parity. Improving farrowing rate using selection can be highly profitable for commercial herds as it results in a permanent change in the genetic composition of the pig population. In Chapter 3 genetic parameters were presented for farrowing rate of the Dutch dam line, the International Large White dam line, and their reciprocal crosses, based on data from Spain and Portugal. Estimated heritability of farrowing rate was 0.07 (se = 0.01) for sows from the Dutch line, 0.07 (se = 0.01) for sows from the International Large White line, and 0.02 (se = 0.01) for sows from the reciprocal cross between the Dutch and the International Large White line. Commercial production pigs are crossbreds farmed all over the world. In contrast, selection is practiced mainly in temperate climates, in nucleus herds using purebred pigs. The success of selection depends on how much genetic progress is realized in crossbred pigs and not in the purebred populations. Genetic correlations for farrowing rate between purebred and crossbreds were below 0.6, which implies that genetic selection only based on purebred data will not breed the best crossbreds. Therefore pig breeding programs have to use a combined crossbred-purebred selection method to make sure genetic improvement is fully realized in commercial crossbred pigs.

In Chapter 2 it was suggested that there is genetic variation for the response in reproductive performance against high temperatures. Therefore in Chapter 3, heritability for the random regression slope of farrowing rate against increasing temperature at day of insemination (= heat tolerance) and the genetic correlation between farrowing rate and heat tolerance were estimated. Heritability estimates for farrowing rate were 0.05 (se = 0.01) for Dutch line sows and 0.08 (se = 0.01) for

International Large White line sows. Heritability estimates for heat tolerance at 29°C were 0.04 (se = 0.01) for Dutch line sows and 0.02 (se = 0.01) for International Large White line sows.

Genetic correlations between farrowing rate and heat tolerance were around 0. Based on these results it could be concluded that there are possibilities for genetic improvement for heat tolerance as expressed in farrowing rate.

In Chapter 2 and Chapter 3 only the effect of heat stress on day of insemination on reproductive performance was considered. However, it can also be postulated that heat stress before or after day of insemination could also have a significant impact on reproductive performance. Therefore in Chapter 4 the effect of different measures of heat stress during each day of the reproduction cycle of Dutch line sows on farrowing rate and total born was investigated using data from Spain and Portugal. Maximum temperature was found to be the measurement of heat stress with largest impact. Additionally it was found that heat stress had a stronger effect on farrowing rate and total born of gilts than of sows. The key period during the reproduction cycle of the gilt / sow is 21 – 14 days prior to first insemination for farrowing rate. Heat stress during this period had largest impact on farrowing rate. Heat stress in the period between 7 days prior to successful insemination until 12 days after had largest impact on total born. Correlations between temperatures on consecutive days were extremely high (> 0.9). Therefore, for ease of interpretation for farrowing rate the maximum temperature on 21 days before first insemination and for total born the maximum temperature at day of successful insemination can be used as predictive measures of heat stress in commercial farms.

The pork supply chain is built around productivity and efficiency in many areas of pig production including sow efficiency. Sow productivity depends on a number of related traits, such as litters per sow per year, number of weaned piglets per sow per year, and length of productive live. Traditionally pig breeding programs have improved sow productivity by focusing on increasing number weaned piglets per sow per year. To improve herd-level litters per sow per year a new trait was proposed in Chapter 5 called problem free sow production (PFSP) by parity, which incorporates the traits interval weaning first insemination, non-return rate, farrowing rate, and selection for next parity. Data on 22,759 insemination records from 4,398 Dutch line sows was available from January 2002 until December 2011 raised in Spain and Portugal. Average level of PFSP was 61%, implying that 39% of sows do not remain problem-free within one parity. Heritability estimate for PFSP was 0.06 (se = 0.01). Genetic correlation between PFSP and general sow reproduction was close to 0, implying that PFSP and sow reproduction can be simultaneously improved via genetic selection. Genetic correlation between PFSP

in heat challenged and temperate conditions was high (>0.9), which implies that pigs with the best performance in a hot climate will also be the best in a temperate climate. Problem free sow production is a trait which can be improved via genetic selection which will result in a reduction of non-productive sow days, in sows that require fewer farmer interventions and ultimately result in an increased number of litters per sow per year.

To conclude, in this thesis it has been shown that it is possible to select for improved heat resistance in addition to improved production levels. However, it has also been shown that genetic correlation between production in temperate and hot climates is high. This implies that within-line pigs with the best performance in a hot climate will be the best in temperate climate too. Therefore, in the context of a commercial breeding company with a crossbred evaluation program breeding for improved heat stress resistance is not necessary. Critical to the long term success of a pig breeding program is to define appropriate breeding goals which are based on the environment that market pigs are expected to perform in and to include crossbred performance data in the selection of purebred pigs. Then these data collection for genetic evaluation needs to be done in that specific environment and this will favour pigs which are able to produce in that specific environment.

Samenvatting

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Wereldwijd neemt de gemiddelde grootte van varkensbedrijven toe en neemt de hoeveelheid beschikbare arbeid per zeug / slachtvarken af. Dit vraagt om zeugen die minder management interventies nodig hebben en die dagelijks gemakkelijk te managen zijn. Naast gemakkelijk te managen, moeten zeugen een groter aanpassingsvermogen hebben omdat wordt verwacht dat de temperatuur wereldwijd gaat stijgen (1.8°C tot 4.0°C tijdens de komende 90 jaar) en dat de varkensvleesproductie gaat verschuiven naar warmere klimaten. Het eindresultaat is dat *commerciële* varkens mogelijk meer last krijgen van hittestress tijdens hun productieve leven. Gedurende de laatste jaren is het aantal varkensfokprogramma's verminderd en er wordt verwacht dat dit in 2020 nog verder zal zijn verminderd. Dit leidt waarschijnlijk (gezien de huidige verscheidenheid in varkensstallen) tot een kleiner aantal varkensfokkerijorganisaties die varkens produceren voor veel verschillende commerciële milieus. Deze milieus variëren in stalontwerp, hoogte, temperatuur, voerkwaliteit, gezondheidsstatus en (varkens)management. Het doel van dit proefschrift was het krijgen van meer inzicht in de genetische aspecten van hitte stress gevoeligheid, kenmerken van gemakkelijk te managen zeugen en worpgrootte en afbigpercentage van de zeug.

Reproductie is van groot belang in zeugenlijnen van commerciële varkensfokprogramma's. Hittestress heeft een negatief effect op reproductie. Varkens hebben last van hittestress wanneer de temperatuur boven de bovenste kritieke temperatuur van de thermo-neutrale zone komt. De thermo-neutrale zone is het gebied van temperaturen tussen de onderste kritieke temperatuur en de bovenste kritieke temperatuur. Boven de bovenste kritieke temperatuur en onder de onderste kritieke temperatuur verbruikt een varken energie om de lichaamstemperatuur op peil te houden. In Hoofdstuk 2 werden verschillen in de relatie tussen temperatuur en reproductie tussen twee verschillende zeugenlijnen onderzocht. En werden de bovenste kritieke temperaturen voor reproductie kenmerken van deze twee verschillende zeugenlijnen vastgesteld. Gegevens van afbigpercentage, worpgrootte en worpgrootte uit eerste dekking werden tussen 2003 en 2005 verzameld in Spanje en Portugal. De zeugen kwamen uit twee verschillende zuivere zeugenlijnen genaamd *"Dutch"* (een Yorkshire zeugenlijn, oorspronkelijk geselecteerd in Nederland) en *"International"* (een Large White zeugenlijn, geselecteerd op basis van wereldwijde gegevens). De gegevens van de eerste inseminatie van de zeug werden gebruikt en gekoppeld aan de maximale buiten temperatuur op de dag van de inseminatie, dit werd gedaan per pariteit. De bovenste kritieke temperatuur voor de reproductie kenmerken van de zeugen uit de “Dutch” lijn lag rond 20°C. Boven die temperatuur daalde het afbigpercentage met 1% per °C, worpgrootte daalde met 0.05 big per °C en worpgrootte uit eerste dekking daalde met 0.13 big per °C. Het afbigpercentage van zeugen van de “International” lijn werd niet beïnvloed door temperatuur. Worpgrootte en worpgrootte uit eerste dekking van zeugen van de “International” lijn werd negatief beïnvloed door temperatuur, maar dit effect was minder sterk dan bij zeugen van de “Dutch” lijn. Bij temperaturen onder de 23°C was afbigpercentage hoger en worpgrootte en worpgrootte uit eerste dekking groter bij zeugen van de “Dutch” lijn dan bij zeugen van de “International” lijn. Boven de 24°C was worpgrootte bijna gelijk in beide zeugenlijnen. Boven de 25°C was afbigpercentage en worpgrootte uit eerste dekking groter voor zeugen van de “International” lijn dan voor zeugen van de “Dutch” lijn. De resultaten uit Hoofdstuk 2 impliceren dat er belangrijke verschillen zijn in de relatie tussen temperatuur en reproductiekenmerken tussen twee genetisch verschillende zeugenlijnen. Deze verschillen suggereren dat genetische selectie op hittestress tolerantie mogelijk is.

Doorgaand op het voorgaande onderzoek werd opgemerkt dat drachtig worden en drachtig blijven een uitdaging is voor zeugen in een warm of heet klimaat. De varkensketen heeft behoefte aan een stabiele en ongestoorde varkensproductie, ongeacht de buitentemperatuur. Afbigpercentage kan worden gedefinieerd als afbiggen van eerste inseminatie binnen één pariteit. Het verbeteren van het afbigpercentage via fokkerij kan zeer gunstig zijn voor commerciële bedrijven, omdat dit resulteert in een permanente verandering in de genetische samenstelling van de varkenspopulatie. In Hoofdstuk 3 werden genetische parameters gepresenteerd van het afbigpercentage van de “Dutch” zeugenlijn, van de “International” zeugenlijn en van hun kruisingen (“Dutch” × “International” en “International” × “Dutch”). Data was beschikbaar uit Spanje en Portugal. De geschatte erfelijkheidsgraad voor afbigpercentage van zeugen van de “Dutch” lijn was 0.07 (standaardfout 0.01), voor zeugen van de “International” lijn was dat 0.07 (standaardfout 0.01) en van zeugen van de kruisingen tussen de “Dutch” lijn en de “International” lijn was dat 0.02 (standaardfout 0.01). Commerciële zeugen op varkensbedrijven over de hele wereld zijn kruisingen. Daarentegen wordt selectie voornamelijk uitgevoerd in gematigde klimaten, in kernbedrijven gebruik makend van zuivere lijnen. Het succes van selectie is afhankelijk van hoeveel genetische vooruitgang gerealiseerd wordt in commerciële zeugen en niet in populaties van zuivere lijnen. De genetische correlaties voor afbigpercentage tussen zuivere lijns zeugen en kruisingen waren kleiner dan 0.6, wat impliceert dat genetische selectie gebaseerd op uitsluitend zuivere lijns gegevens niet leidt tot de beste commerciële zeugen. Daarom moeten varkensfokprogramma's gebruik maken van de "combined crossbred-purebred selection" methode, opdat genetische verbetering volledig gerealiseerd wordt in commerciële kruisingen.

In Hoofdstuk 2 werd gesuggereerd dat genetische selectie op hittetolerantie welllicht mogelijk is. Daarom werden in Hoofdstuk 3 de erfelijkheidsgraad van de random regressiehelling van afbigpercentage tegen toenemende temperatuur op dag van inseminatie (= hitte tolerantie) en de genetische correlatie tussen afbigpercentage en hitte tolerantie geschat. Geschatte erfelijkheidsgraden voor afbigpercentage was 0.05 (standaardfout 0.01) voor zeugen van de "Dutch" lijn en 0.08 (standaardfout 0.01) voor zeugen van de "International" lijn. Geschatte erfelijkheidsgraden van hitte tolerantie bij 29°C waren 0.04 (standaardfout 0.01) voor zeugen van de "Dutch" lijn en 0.02 (standaardfout 0.01) voor zeugen van de "International" lijn. Genetische correlaties tussen afbigpercentage en hitte tolerantie lagen rond 0. Gebaseerd op deze resultaten kan worden geconcludeerd dat er mogelijkheden zijn voor genetische verbetering van hitte tolerantie uitgedrukt in afbigpercentage.

In Hoofdstuk 2 en 3 werd alleen gekeken naar het effect van hittestress op dag van inseminatie op reproductie. Echter hittestress voor of na inseminatie zou ook effect kunnen hebben op reproductie. Daarom werd in Hoofdstuk 4 het effect van verschillende weersvariabelen, op elke dag van de reproductie cyclus van de zeug, op afbigpercentage en worpgrootte onderzocht. Data uit Spanje en Portugal was beschikbaar voor zeugen van de "Dutch" lijn. Er werd gevonden dat van de weersvariabelen, maximum temperatuur de grootste impact heeft op reproductie. Daarnaast werd gevonden dat hittestress een groter effect op gelten heeft dan op zeugen, met betrekking tot afbigpercentage en worpgrootte. Voor afbigpercentage was de belangrijkste periode in de cyclus van de gelt / zeug de periode van 21 – 14 dagen voor de eerste inseminatie. Hitte stress tijdens deze periode heeft de grootste invloed op afbigpercentage. Voor worpgrootte heeft hittestress in de periode van 7 dagen voor tot 12 dagen na succesvolle inseminatie de grootste invloed. Correlaties tussen temperaturen op opeenvolgende dagen waren extreem hoog (> 0.9). Vanwege interpretatiegemak kan daarom gebruik worden gemaakt van de maximum temperatuur op 21 dagen voor eerste inseminatie voor afbigpercentage en maximum temperatuur op dag van succesvolle inseminatie voor worpgrootte als voorspellende waarden voor hittestress op commerciële bedrijven.

De varkensketen is gebouwd rondom productiviteit en efficiëntie. Productiviteit van zeugen is afhankelijk van een aantal gerelateerde kenmerken zoals aantal worpen per zeug per jaar, aantal gespeende biggen per zeug per jaar en levensduur van de zeug. Varkensfokprogramma's hebben traditioneel de productiviteit van de zeug vergroot door te focussen op het verhogen van het aantal gespeende biggen per zeug per jaar en levensduur van de zeug. Om op bedrijfsniveau het aantal worpen per zeug per jaar te verbeteren werd in Hoofdstuk 5 een nieuw kenmerk voorgesteld, genaamd probleem vrije zeugen productie (problem free sow production; PFSP) per pariteit. Dit kenmerk bevatte de kenmerken interval spenen tot eerste inseminatie, non-return percentage, afbigpercentage en geselecteerd worden voor de volgende pariteit. Data van 22.759 inseminatiegegevens van 4.398 zeugen van de "Dutch" lijn, in Spanje en Portugal, waren beschikbaar over een periode van januari 2002 tot december 2011. Het gemiddelde niveau van PFSP was 61%, wat betekent dat 39% van de zeugen niet probleem-vrij blijft binnen één pariteit. De geschatte erfelijkheidsgraad voor PFSP was 0.06 (standaardfout 0.01). De genetische correlatie tussen PFSP en algemene reproductie van de zeug was bijna 0, wat impliceert dat PFSP en reproductie van de zeug gelijktijdig verbeterd kan worden via genetische selectie. De genetische correlatie tussen PFSP onder hittestress en onder gematigde condities was hoog (> 0.9), wat betekent dat varkens die, binnen een lijn, het beste presteren in een heet klimaat ook de beste zullen zijn in een gematigd klimaat. Via genetische selectie kan het kenmerk PFSP worden verbeterd en dat zal resulteren in een vermindering van het aantal non-productieve dagen van de zeug, in zeugen die minder interventies door de varkenshouder nodig hebben en uiteindelijk in een verhoogd aantal worpen per zeug per jaar.

Tot slot, dit proefschrift laat zien dat het mogelijk is om te selecteren op verbeterde hitte resistentie in aanvulling op selectie op productie. De genetische correlatie tussen productie in een gematigd klimaat en productie in een heet klimaat is hoog, wat impliceert dat varkens die het beste presteren, binnen een zeugenlijn, in een heet klimaat ook het beste presteren in een gematigd klimaat. Daarom is het voor commerciële varkensfokkerijorganisaties die gegevens van commerciële zeugen meenemen in het fokprogramma niet nodig om op verbeterde hittestress resistentie te fokken. Voor het lange termijn succes van een varkensfokprogramma is het van belang om een passend fokdoel te definiëren, dat gebaseerd is op de omgeving waarin commerciële varkens moeten presteren, en om gegevens van de prestaties van commerciële varkens te gebruiken voor de selectie in de zuivere lijnen. De dataverzameling voor genetische evaluatie dient plaats te vinden in die specifieke omgeving, zodat die varkens die het beste produceren in die omgeving worden geselecteerd.

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Saskia

Curriculum Vitae

Curriculum Vitae

Saskia Bloemhof-Abma is geboren op 17 Juni 1983 in Sint Annaparochie, in de provincie Friesland, en groeide op in Sint Jacobiparochie. In 2000 behaalde ze haar HAVO diploma aan het Christelijk Scholengemeenschap Comenius te Leeuwarden. Datzelfde jaar begon ze aan de hbo-studie Dier- en Veehouderij met als specialisatie Diergezondheidszorg aan het Van Hall Instituut in Leeuwarden. In 2004 haalde zij haar diploma, waarna ze in september 2005 begon aan de masters opleiding Dierwetenschappen aan Wageningen Universiteit, met als specialisatie “Fokkerij en Genetica”. Twee afstudeervakken werden uitgevoerd. De eerste bij het toenmalige NRS in Arnhem gericht op de genetische achtergrond van klinische mastitis in melkvee. De tweede bij het Institute for Pig Genetics (IPG B.V.) gericht op verschillen tussen zeugenlijnen in hun respons op hittestress. In 2007 studeerde ze af waarna ze begon als onderzoeker bij IPG. In oktober 2008 begon ze in combinatie met haar baan als onderzoeker bij IPG aan haar promotie onderzoek bij het “Animal Breeding and Genomics Centre’ waarvan de resultaten beschreven zijn in dit proefschrift. Sinds 2013 is ze werkzaam als geneticus bij de afdeling “Global genetic services” van PIC.

Curriculum Vitae

Saskia Bloemhof-Abma was born on June 17 1983 in Sint Annaparochie, the Netherlands. She was raised in Sint Jacobiparochie and in 2000 she graduated from high school Christelijk Scholengemeenschap Comenius Leeuwarden. In the same year she started her BSc Animal Sciences at Van Hall Instituut in Leeuwarden. In 2004 she graduated and in 2005 she started with the MSc Animal Sciences at Wageningen University, with the specialization “Animal Breeding and Genetics”. She performed one major thesis at the NRS in Arnhem, which studied the genetic background of clinical mastitis in Holstein Friesian dairy cattle. A second major thesis was performed at the Institute for Pig Genetics (IPG B.V.) on differences between dam lines in response to heat stress. After finishing her MSc in 2007 she started working as researcher at IPG. In October 2008 she started, next to her job as researcher at IPG, her PhD study at the Animal Breeding and Genomics Centre in Wageningen. The results of this research are described in this thesis. Since 2013 she is working as geneticist at the “Global genetic services” department at PIC.

Publications

Peer reviewed articles

Bloemhof, S., P.K. Mathur, E.F. Knol, E. F., and E.H. Van der Waaij. 2013. Effect of daily environmental temperature on farrowing rate and total born in dam line sows. Journal of Animal Science 91:2667-2679.

Bloemhof, S., A. Kause, E.F. Knol, J.A.M. Van Arendonk, and I. Misztal. 2012. Heat stress effects on farrowing rate in sows: Genetic parameter estimation using within-line and crossbred models. Journal of Animal Science 90:2109-2119.

Mathur, P. K., J. ten Napel, S. Bloemhof, L. Heres, E.F. Knol, and H.A. Mulder. 2012. A human nose scoring system for boar taint and its relationship with androstenone and skatole. Meat Science 91:414-422.

Bloemhof, S., G. de Jong, and Y. de Haas. 2009. Genetic parameters for clinical mastitis in the first three lactations of Dutch Holstein cattle. Veterinary Microbiology 134:165-171.

Merks, J.W.M., E.H.A.T. Hanenberg, S. Bloemhof, and E.F. Knol. 2009. Genetic opportunities for pork production without castration. Animal Welfare 18:539-544.

Bloemhof, S., E.H. van der Waaij, J.W.M. Merks, and E.F. Knol, 2008. Sow line differences in heat stress expressed in reproductive performance traits. Journal of Animal Science 86:3330-3337.

Abstracts in conference proceedings

Bloemhof, S., E.F. Knol, E.H. van der Waaij, and I. Misztal. 2012. Towards robust sows: Heat tolerance expressed in fecundity. Joint ASAS ADSA CSAS Meeting Phoenix, Arizona USA. Abstract 817.

Bloemhof, S., E.F. Knol, A. Kause, and I. Misztal. 2010. Application of a crossbred model reveals additional genetic variation in reproduction traits of commercial females. Joint ASAS ADSA CSAS Meeting Denver, Colorado USA. Abstract 430.

Knol, E.F., S. Bloemhof, L. Heres, and G. Tacken. 2010. Selection against boar taint: Slaughter line panel and consumer perceptions. *In:* Proc. 9th Wold Congr. Genet. Appl. Livest. Prod., Leipzig Germany.

Merks, J.W.M., S. Bloemhof, P.K. Mathur, and E.F. Knol. 2010. Quantitative genetic opportunities to ban castration. *In:* Book of abstracts of the 61st Meeting of the European Association for Animal Production, Heraklion, Greece.

Bloemhof, S., E.F. Knol, and I. Misztal. 2009. Genetic parameters of heat stress tolerance in sows. ASAS Midwest Meeting Des Moines, Iowa USA. Abstract 34.

Haas, de Y., S. Bloemhof, W. Ouweltjes, J. ten Napel, and G. de Jong. 2007. Improving selection on udder health by using different trait definitions of somatic cell count. *In:* Interbull bulletin.

Bloemhof, S., Y. de Haas, and G. de Jong. 2007. Genetic parameters for clinical mastitis in primi- versus multiparous cows. *In:* Proceedings of the Heifer Mastitis Conference, Gent Belgium. Abstract 28.

Other publications

Bloemhof, S. 2012. Selecting for heat tolerance for better farrowing rates. Pig Progress Volume 26 No 6: 22-23.

Bloemhof, S. 2011. Beating heat stress by choosing the right sow. Pig Progress Volume 27 No 4: 18-19.

Training and Supervision plan

Training and Supervision plan

Basic package (3 ECTS)

WIAS Introduction Course	2009
Course on philosophy of science and/or ethics, June 20-22	2012

Scientific exposure (11 ECTS)

International conferences

PBRT, Canterbury, UK, April 21-23	2008
ASAS Midwest, Des Moines, USA, March 16-18	2009
ASAS, Denver, USA, July 11-15	2010
2nd Symposium Low Input Breeds, Hammamet, Tunisia, May 15-18	2012
ASAS, Phoenix Arizona, USA, July 15-19	2012

Seminars and workshops

F&G connection days, Vught, November 27-28	2008
F&G connection days, Vught, November 25-26	2010

Presentations

Line differences in heat stress expressed in fertility traits, Canterbury, UK April 22, oral	2008
Genetic parameters of heat stress tolerance in sows, Des Moines, USA, March, oral	2009
Application of a crossbred model reveals additional genetic variation in reproduction traits of commercial fermales, ASAS, July, oral	2010
Genetic aspects of heat stress in pigs expressed in fertility traits, Low Input Breeds, Tunisa, oral	2012
Towards robust sows: Heat tolerance expressed in fecundity traits, ASAS July 2012, oral	2012

In-depth studies (8 ECTS)

Disciplinary and interdisciplinary courses

Quantitative genetics, Wageningen, June 7-11	2010
Genomic computing using single-step methodology, Georgia, USA, May 28-June 1	2012

Advanced statistics courses

Programming in Animal Breeding, University of Georgia, Athens, USA May 13-June 3	2008

Professional skills support courses (4 ECTS)

Course Techniques for Scientific Writing, December 15-18	2009
Career Assesment, August 14	2012
Interdisciplinary research, November 11 and 15, December 2	2010

Research skills training (8 ECTS)

Preparing own PhD research proposal	2009
External training period, University of Georgia, Athens, USA February 16-April 15	2009

Didactic skills training (4 ECTS)

MSc, Major Thesis ADP Willemien van de Kandelaar	2008
MSc, Major Thesis Carla Martins	2010

Education and training total: 37 ECTS

Colophon

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