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Genetic variation for farrowing rate in pigs in response to change in photoperiod and ambient temperature

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ABSTRACT: Seasonal infertility is often observed as anestrus and a lower conception rate resulting in a reduced farrowing rate (FR) during late summer and early autumn. This is often regarded as an effect of heat stress; however, we observed a reduction in the FR of sows even after correcting for ambient temperature in our data. Therefore, we added change in photoperiod in the analysis of FR considering its effect on sow fertility. Change in photoperiod was modeled using the cosine of the day of first insemination within a year. On an average, the FR decreased by 2% during early autumn with decreasing daily photoperiod compared with early summer with almost no change in daily photoperiod. It declined 0.2% per degree Celsius of ambient temperature above 19.2°C. This result is a step forward in disentangling the 2 environmental components responsible for seasonal infertility. Our next aim was to estimate the magnitude of genetic variation in FR in response to change in photoperiod and ambient temperature to explore opportunities for selecting pigs to have a constant FR throughout the year. We used reaction norm models to estimate additive genetic variation in response to change in photoperiod and ambient temperature. The results revealed a larger genetic variation at stressful environments when daily photoperiod decreased and ambient temperatures increased above 19.2°C compared with neutral environments. Genetic correlations between stressful environments and nonstressful environments ranged from 0.90 (±0.03) to 0.46 (±0.13) depending on the severity of the stress, indicating changes in expression of FR depending on the environment. The genetic correlation between responses of pigs to changes in photoperiod and to those in ambient temperature were positive, indicating that pigs tolerant to decreasing daily photoperiod are also tolerant to high ambient temperatures. Therefore, selection for tolerance to decreasing daily photoperiod should also increase tolerance to high ambient temperatures or vice versa.

Key words: ambient temperature, farrowing rate, photoperiod, pig, reaction norm, seasonal infertility

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INTRODUCTION

Seasonal infertility affects many farms around the world and is manifested by anestrus or a lower conception rate resulting in a reduced farrowing rate (**FR**) and a prolonged weaning-to-estrus interval (Peltoniemi et al., 1999; Anil et al., 2005; Chokoe and Siebrits, 2009; Auvigne et al., 2010). Efforts are made to overcome the adverse effect of environment through management measures, such as special housing, light regimens, and cooling or heating systems. However, a decline in fertility during late summer and early autumn is observed in many farms around the world despite all these management measures, and it is commonly known as seasonal infertility (Auvigne et al., 2010).

Seasonal infertility is observed at the same time when the European wild sow experiences total anestrus to avoid farrowing during midwinter (Tast et al., 2001; Almond and Bilkei, 2005). Changing photoperiod is thought to provide the primary cue for determining the season when reproductive activity is most appropriate (Peltoniemi et al., 1999). For instance, periods with decreasing daily photoperiod, for example, September/October, is an unfavorable season for reproduction (Tast et al., 2001). Despite domestication, sows still exhibit a seasonal trend in their reproductive performance related to photoperiod, and the domestic sow is

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able to recognize and respond to the changes in natural photoperiod in a controlled pig husbandry system (Tast et al., 2001; Hälli et al., 2008; Auvigne et al., 2010).

Detrimental effect of high ambient temperature on FR was shown by Bloemhof et al. (2013). High ambient temperatures, however, do not correlate with the time of the year when seasonal infertility is observed (Tast et al., 2002). High ambient temperatures might intensify the negative effect of decreasing daily photoperiods, but it is unlikely to be the main trigger of seasonal infertility in temperate climates (LeMoine, 2013).

Breeding organizations aim to provide sows with constant fertility despite seasonal variation. To implement genetic selection for sows that are tolerant to changes in photoperiod and ambient temperatures, we need to determine the magnitude of genetic variation in response to these factors. Bloemhof et al. (2012) showed that genetic variation for FR in response to ambient temperature variation exists. It is unknown if genetic variation for FR in response to photoperiod variation exists and if response to photoperiod variation interacts with response to ambient temperature variation. The aims of this study, therefore, were 1) to model and evaluate the effect of change in photoperiod on FR apart from the effect of ambient temperature, 2) to estimate the additive genetic variation among pigs for FR in response to changes in photoperiod, and 3) to estimate the genetic correlation between responses of pigs to changes in photoperiod and ambient temperature.

MATERIALS AND METHODS

Data Set

Reproductive records were available from Topigs Norsvin farms located in 14 countries in the Northern Hemisphere. The data set consisted of 60,624 mating records from 17,070 sows and their subsequent farrowing information recorded from April 2000 until February 2014. Most of the sows (12,418 out of 17,070) had more than 1 observation. Sows originated from 2 Large White dam lines, International Large White and Dutch Large White. Each record included sow identification number, parity, farm, country, date of first insemination, date of successful insemination, service sire, farrowing date, gestation length, FR, litter size, number of piglets born alive, and number of stillborn piglets. The FR of each sow was scored as 100 or 0. The FR was 100 if the first insemination led to a gestation longer than 108 d and at least 1 piglet was born. Otherwise, the FR was considered 0. Observations for litter size and gestation length were removed if they were smaller or larger than the mean ± 3 median absolute deviation. Observations, therefore, were removed from the data set when litter size was smaller than 5 piglets or larger than 21 piglets or when gestation length was smaller than 109 d or larger than 119 d. Only farms with more than 100 observations were kept. Disease outbreaks were detected as in Mathur et al. (2014), and observations recorded during a disease outbreak were removed from the data set to avoid confounding effects with environmental stress. Observations without ambient temperature records were removed from the original data set. For all phenotyped sows, pedigree information was collected up to 20 generations back, which included 91,233 animals.

Ambient Temperature

Meteorological data were obtained from the Koninklijk Nederlands Meteorologisch Instituut (KNMI, 2015) for Dutch farms and from the National Oceanic and Atmospheric Administration National Data Center Climate Data Online (NCDC, 2015) for all other farms. Each farm was assigned to the nearest weather station. Most of the farms had a weather station within 60 km of the farm, with the closest being 5.4 km and the farthest being 250 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. They concluded that for the purpose of genetic studies related to heat stress, the information from weather stations may be as accurate in capturing the effect of heat stress as the data collected on farm (Freitas et al., 2006). Each insemination record in our data set was assigned the daily maximum temperature from the nearest weather station on the 21st day before a sow's first insemination. According to the study of Bloemhof et al. (2013), maximum temperature on 21 d before first insemination can be used as predictive measures of heat stress in commercial sow farms. Maximum ambient temperatures were used to estimate heat load. Heat load was defined as the positive difference between the maximum ambient temperature and the upper critical temperature (**UCT**) of the sows. A UCT of 19.2°C for FR was used following Bloemhof et al. (2008). A plateau-linear function was fitted considering effect of ambient temperature as a plateau when ambient temperature was less than or equal to UCT and linear when ambient temperature was greater than UCT (Bloemhof et al., 2013).

Photoperiod Function

Sows at the insemination barn received a combination of natural and artificial light. The time and intensity of artificial lighting was not available. However, windows in the barns made that photoperiod perceived by the sows follow the natural one, especially for days

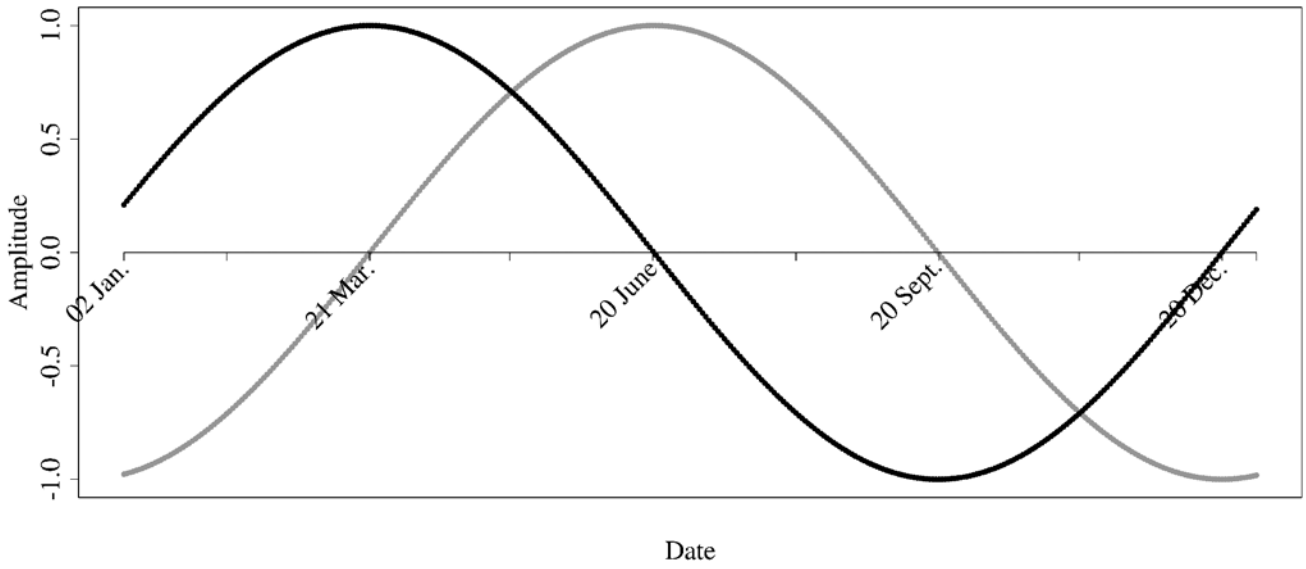

Figure 1. Photoperiod modeled as a function of date within a year using a sine function (gray line) and change in photoperiod modeled as a function of date within a year using a cosine function (black line).

with daylight longer than 8 h. Photoperiod was modeled by taking the sine of the day of first insemination within a year. We used June 21 as the longest day of the year and March 21 as the March equinox for the Northern Hemisphere and modeled the peak of the sine curve to match June 20 and the inflection point where the sine function is 0 at March 21, as suggested by Bergsma and Hermesch (2012). However, sows adapt their fertility behavior as a response to changes in photoperiod (Tast et al., 2000). The first derivative of photoperiod at days of first insemination gives the change in photoperiod at day of first insemination, which is the cosine function of the photoperiod function (Fig. 1). The change in photoperiod is largest at the start of spring with cosine function values of 1.0 (i.e., maximum at March 21), meaning increased photoperiod after many days with short photoperiods, and at the start of autumn (i.e., minimum at September 21) with cosine function values of −1.0, meaning decreased photoperiod after many days on long photoperiods. Therefore, the change in photoperiod is modeled as

$$\text{change in photoperiod} = \cos\{[(\text{day of first insemination} - \text{March 21})/365] \times 0.25 \times 2\pi\}.$$

Sows might recognize earlier or later changes in photoperiod; therefore, to identify when exactly sows perceive the change in photoperiod, we analyzed the effect of shifting the inflection point of photoperiod 30 d before and 30 d after March 21. For each day, the effect of change in photoperiod on FR was estimated based on REML analyses using the software ASReml (Gilmour et al., 2009). Significance was based on a Wald test. The following linear model for FR was used (base linear model number 1 [$\mathbf{M_1}$]):

$$\mathbf{y = Xb + Za_i + Zpe + Ws + e}, \quad [1]$$

in which **y** is a vector of sow FR; **b** is a vector of fixed effects that included interaction of line of the sow (2 classes) with farm (14 classes), interaction line of the sow (2 classes) with parity of the sow (8 classes, with class 8 including parities 8 or more), litter type (2 classes, purebred or crossbred), year within farm (306 classes), regression coefficient on ambient temperature at 21 d before a sow's first insemination, and regression coefficient on change in photoperiod modeled with the cosine function; $\mathbf{a_i}$ is a vector of random additive genetic effects for intercept with $\mathbf{a_i} \sim N(\mathbf{0}, \mathbf{A}\,\sigma^2_{a_i})$, in which $\sigma^2_{a_i}$ is the additive genetic variance for intercept and **A** is a matrix of additive genetic relationships among pigs; **pe** is a vector of random permanent environmental effects with $\mathbf{pe} \sim N(\mathbf{0}, \mathbf{I}\,\sigma^2_{a_{pe}})$, in which $\sigma^2_{a_{pe}}$ is the permanent environmental variance and **I** is an identity matrix; **s** is a vector of random service sire effects with $\mathbf{s} \sim N(\mathbf{0}, \mathbf{I}\,\sigma^2_s)$, in which σ^2_s is the service sire variance; **e** is a vector of residuals; and **X**, **Z**, and **W** are the design matrices assigning the observations to the levels of fixed and random effects.

Definition of Tolerance to Environmental Stress

The decreases in FR showed a seasonal pattern, which were was related to decreased photoperiod after many days on long photoperiods and high ambient temperatures (Peltoniemi et al., 1999; Tast et al., 2001; Almond and Bilkei, 2005; Auvigne et al., 2010). Variation in FR in response to changes in photoperiod or ambient temperature, however, may be different between pigs, and part of this variation might be genetic. Genetic variation for FR in response to changes

in photoperiod or ambient temperature variation means the existence of genotype × environment interaction (**G×E**), that is, nonparallel reaction norms. Bloemhof et al. (2012) showed that pigs react differently to ambient temperature resulting in G×E. Likewise, G×E with 2 covariates, changes in photoperiod and ambient temperature, would show how pigs genetically respond to 2 environmental factors. "Long-day tolerance" was defined as the relative change in FR when photoperiod decreases after many days on long photoperiods modeled with the cosine function. Heat tolerance was defined as the relative change in FR per unit increase in ambient temperature above the UCT (19.2°C).

Genetic Analysis

Initially, the base model (M_1) was used. This was followed by reaction norm models, in which the genetic effect of the reaction norms on change in photoperiod and on ambient temperature were added one at a time to the base model. The final model was as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za_i} + \mathbf{Z_{ph}a_{ph}} + \mathbf{Z_t a_t} + \mathbf{Zpe} + \mathbf{Ws} + \mathbf{e}, \quad [2]$$

in which the vectors **y**, **b**, $\mathbf{a_i}$, **pe**, and **s** as well as the matrices **X**, **Z**, and **W** are defined as in the basic linear model [1]; $\mathbf{a_{ph}}$ is a vector of random additive genetic effects for slope of the reaction norm lines of FR on change in photoperiod; and $\mathbf{a_t}$ is a vector of genetic random effects for slope of the reaction norm lines of FR on ambient temperature. Matrices $\mathbf{Z_{ph}}$ and $\mathbf{Z_t}$ are design matrices assigning change in photoperiod and ambient temperature, respectively, to the slopes of the reaction norm lines. The additive genetic effects ai, aph, and at are multivariate normally distributed $N\left(\begin{matrix}\mathbf{0}\\ \mathbf{0}\\ \mathbf{0}\end{matrix}, \mathbf{G_{RN}} \otimes \mathbf{A}\right)$, in which $\mathbf{G_{RN}} = \begin{bmatrix} \sigma^2_{a_i} & \sigma_{a_i,a_{ph}} & \sigma_{a_i,a_t} \\ \sigma_{a_i,a_{ph}} & \sigma^2_{a_{ph}} & \sigma_{a_{ph},a_t} \\ \sigma_{a_i,a_t} & \sigma_{a_{ph},a_t} & \sigma^2_{a_t} \end{bmatrix}$, in which $\sigma^2_{a_{ph}}$ is the additive genetic variance for change in photoperiod slope; $\sigma^2_{a_t}$ is the additive genetic variance for ambient temperature slope; $\sigma_{a_i,a_{ph}}$ is the additive genetic covariance between additive genetic effect on intercept and change in photoperiod slope; σ_{a_i,a_t} is the additive genetic covariance between additive genetic effect on intercept and ambient temperature slope; and σ_{a_{ph},a_t} is the covariance between genetic effect on change in photoperiod slope and ambient temperature slope. The residual variance was considered to be heterogeneous along the environmental gradients of temperature and change in photoperiod. For that, 5 environmental classes were created. Although ambient temperatures tend to increase when daily photoperiod decreases, we observed variation in change in photoperiod per range of ambient temperature. Therefore, we were not able to group the observations according to ambient temperature and change in photoperiod simultaneously. As a result, observations were separately grouped in 2 ways: 1) according to ambient temperature and 2) according to change in photoperiod. Observations were sorted according to ambient temperature from coldest to warmest to classify observations into 5 environmental classes. The first environmental class consisted of observations with ambient temperatures lower than or equal to the UCT (19.2°C), and the remaining observations were divided in 4 classes considering quartiles (Table 1). For change in photoperiod, the observations were arranged from 1 to −1 to group them into the 5 environmental classes considering quintiles (Table 1). For each of the 5 environmental classes a residual variance was defined, so that , in which $\text{var}\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\\ \vdots\\ \mathbf{e}_5\end{bmatrix} = \mathbf{R} \otimes \mathbf{I}$. Variance components were $\mathbf{R} = \begin{bmatrix} \sigma^2_{e_1} & \mathbf{0} & \cdots & \mathbf{0} \\ \mathbf{0} & \sigma^2_{e_2} & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \sigma^2_{e_5} \end{bmatrix}$ estimated using ASReml software (Gilmour et al., 2009). Furthermore, the additive genetic variances due to the changes in photoperiod, ambient temperature, and total were calculated for each of the 5 environmental classes using the variance and covariance estimates from G_{RN}:

$$\sigma^2_{a_{ph_j}} = ph_j^2 \times \sigma^2_{a_{ph}},$$

$$\sigma^2_{a_{t_j}} = t_j^2 \times \sigma^2_{a_t}, \text{ and}$$

$$\sigma^2_{a_{total_j}} = \sigma^2_{a_i} + ph_j^2 \times \sigma^2_{a_{ph}} + t_j^2 \times \sigma^2_{a_t} + 2ph_j \times \sigma_{a_i,a_{ph}} + 2t_j \times \sigma_{a_i,a_t} + 2\left(ph_j \times t_j\right) \times \sigma_{a_{ph},a_t},$$

Table 1. Classification of observations in 5 environmental classes, according to ambient temperature and according to change in photoperiod, to specify heterogeneous residuals in the data[1]

Class	Mean (T)	Min. (T)	Max. (T)	Mean (PH)	Min. (PH)	Max. (PH)	Obs
Ambient temperature[2]							
1	10.45	−24.00	19.20	0.35	−1	1	34,856
2	20.47	19.22	21.70	−0.28	−1	1	6,481
3	23.25	21.72	24.90	−0.39	−1	1	6,414
4	26.91	25.00	29.00	−0.50	−1	1	6,488
5	36.60	29.10	40.70	−0.86	−1	1	6,385
Change in photoperiod[3]							
1	9.26	−24.00	32.50	0.94	0.81	1.00	11,983
2	12.16	−21.70	33.28	0.58	0.31	0.80	12,248
3	16.23	−18.90	39.20	−0.00	−0.30	0.31	11,991
4	21.92	−11.70	39.90	−0.58	−0.81	−0.32	12,198
5	25.15	−9.00	40.70	−0.94	−1.00	−0.81	12,204

[1]Mean, minimum (Min.), and maximum (Max.) ambient temperatures (T) and change in photoperiods (PH) and number of observation (Obs) are presented for each of the 5 environmental classes.

[2]Ambient temperature at 21 d before a sow's first insemination ranged from coldest to warmest, first environmental class consisted of observations with ambient temperatures lower or equal to the upper critical temperature (19.2°C), and remaining observations were divided in 4 classes considering quartiles.

[3]Change in photoperiod at sow's first insemination ranged from 1 to −1 to classify observations in 5 classes considering quintiles.

in which $\sigma^2_{a_{ph_j}}$ is the additive genetic variance due to change in photoperiod at environmental class j, $\sigma^2_{a_{t_j}}$ is the additive genetic variance due to ambient temperature at environmental class j, $\sigma^2_{a_{\text{total}_j}}$ is the total additive genetic variance at environmental class j, and ph_j and t_j are the average change in photoperiod and ambient temperature at environmental class j.

In total, 4 different reaction norm models were used. These were reaction norm models with change in photoperiod and on ambient temperature added one at a time to the base model (M_1) and with different grouping of heterogeneity of residual variance. These are described as reaction norm model numbers 1 through 4 ($\mathbf{RN_1}$ to $\mathbf{RN_4}$) and are summarized in Table 2.

The goodness-of-fit of each reaction norm model was assessed with Akaike information criterion (**AIC**) using the following formula (Akaike, 1973):

$$\text{AIC} = -2\log L + 2K,$$

in which logL is the logarithm of likelihood of the model and K is the number of variables in the model.

The Effect of Environmental Stress on Genetic Variance and Reranking of Pigs

We calculated genetic correlations between FR at a nonstressful environment and FR at each of the 5 environmental classes using the $\mathbf{G_{RN}}$. In addition, the across-environment genetic correlations were estimated with a bivariate model to check whether estimates of the reaction norm models were not artifacts of random regression. With the bivariate model, FR recorded in a nonstressful environment and in a stressful environment were considered different traits. A nonstressful environment was defined as having ambient temperature equal to or lower than 19.2°C and an increase in photoperiod larger than 0.3. A stressful environment was defined as having ambient temperature higher than 23.2°C and a decrease in photoperiod smaller than −0.3. The bivariate model was as follows:

$$\begin{bmatrix} \mathbf{y}_{\text{stress}} \\ \mathbf{y}_{\text{no\_stress}} \end{bmatrix} = \mathbf{Xb} + \begin{bmatrix} \mathbf{Z}_{\text{stress}} & 0 \\ 0 & \mathbf{Z}_{\text{no-stress}} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{\text{stress}} \\ \mathbf{a}_{\text{no\_stress}} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{\text{stress}} & 0 \\ 0 & \mathbf{Z}_{\text{no-stress}} \end{bmatrix} \begin{bmatrix} \mathbf{pe}_{\text{stress}} \\ \mathbf{pe}_{\text{no\_stress}} \end{bmatrix} + \begin{bmatrix} \mathbf{W}_{\text{stress}} & 0 \\ 0 & \mathbf{W}_{\text{no-stress}} \end{bmatrix} \begin{bmatrix} \mathbf{s}_{\text{stress}} \\ \mathbf{s}_{\text{no\_stress}} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\text{stress}} \\ \mathbf{e}_{\text{no\_stress}} \end{bmatrix}, \quad [3]$$

Table 2. Statistical model implemented for analysis of environmental stress, description of the random part, the heterogeneous residual (HR), and goodness-of-fit tested with log-likelihood (LogL) and Akaike information criterion (AIC) for respective model ranking

Model[1]	Random part[2]	HR[3]	LogL	AIC	Ranking
M_1	$\mathbf{a_i} + \mathbf{pe_i} + \mathbf{s}$	*NA*	38,608.66	492.22	***5***
RN_1	$\mathbf{a_i} + \mathbf{pe_i} + \mathbf{a_{ph}} + \mathbf{s}$	*T*	38,829.97	51.60	***2***
RN_2	$\mathbf{a_i} + \mathbf{pe_i} + \mathbf{a_{ph}} + \mathbf{s}$	*PH*	38,760.70	190.14	***4***
RN_3	$\mathbf{a_i} + \mathbf{pe_i} + \mathbf{a_{ph}} + \mathbf{a_t} + \mathbf{s}$	*T*	38,856.77	0.00	***1***
RN_4	$\mathbf{a_i} + \mathbf{pe_i} + \mathbf{a_{ph}} + \mathbf{a_t} + \mathbf{s}$	*PH*	38,822.57	68.40	***3***

[1]M_1 = base linear model number 1; RNx = reaction norm model number x.

[2]$\mathbf{a_i}$ is a vector of random additive genetic effects for intercept; $\mathbf{pe^i}$ is a vector of random permanent environmental effects for intercept; $\mathbf{a_{ph}}$ is a vector of random additive genetic effects for slope of the reaction norm lines of performances on photoperiod; $\mathbf{a_t}$ is a vector of random additive genetic effects for slope of the reaction norm lines of performances on ambient temperature; $\mathbf{s}$ is a vector of random service sire effects.

[3]The heterogeneity of residual variance is grouped by ambient temperature (T), change in photoperiod (PH), or not applicable (NA) because the model is not a reaction norm model.

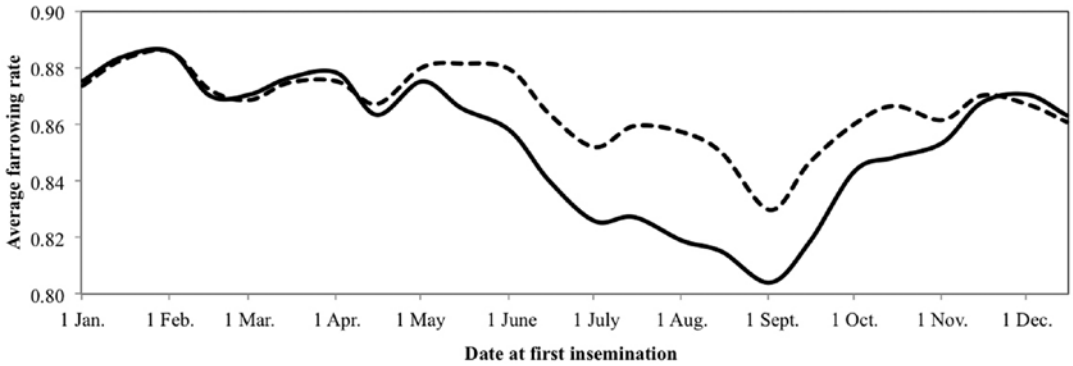

Figure 2. Raw average farrowing rate in relation to the date at first insemination. Dashed line shows the averages after accounting for ambient temperature. Averages are from 15 consecutive years (2000–2014).

in which $\mathbf{y}_{stress}$ ($\mathbf{y}_{no\_stress}$) is a vector of sow performance at stressful environment (nonstressful environment); **b** is a vector of fixed effects as described in model [1]; $\mathbf{a}_{stress}$ ($\mathbf{a}_{no\_stress}$) is a vector of random additive genetic effects in stressful environment (nonstressful environment); $\mathbf{pe}_{stress}$ ($\mathbf{pe}_{no\_stress}$) is a vector of random permanent environmental effects in stressful environment (nonstressful environment); **s**stress ($\mathbf{s}_{no\_stress}$) is a vector of random service sire effects in stressful environment (nonstressful environment); and $\mathbf{e}_{stress}$ ($\mathbf{e}_{no\_stress}$) is a vector of residuals in a stressful environment (nonstressful environment). Matrix **X** is the design matrix assigning the observations to the levels of fixed effects. Matrices $\mathbf{Z}_{stress}$ ($\mathbf{Z}_{no\_stress}$) and $\mathbf{W}_{stress}$ ($\mathbf{W}_{no\_stress}$) are the design matrices assigning the observations to the levels of random effects in a stressful environment (nonstressful environment). Variances for the genetic, permanent environment, sire, and residual effects at each environment were defined as

$$\text{var}\begin{bmatrix}\mathbf{a}_{stress}\\ \mathbf{a}_{no\_stress}\end{bmatrix} = \mathbf{G}\otimes\mathbf{A}, \text{ in which } \mathbf{R} = \begin{bmatrix}\sigma^2_{a_{stress}} & \sigma_{a_{stress},a_{no\_stress}}\\ \sigma_{a_{stress},a_{no\_stress}} & \sigma^2_{a_{no\_stress}}\end{bmatrix},$$

$$\text{var}\begin{bmatrix}\mathbf{pe}_{stress}\\ \mathbf{pe}_{no\_stress}\end{bmatrix} = \mathbf{R}\otimes\mathbf{I}, \text{ in which } \mathbf{R} = \begin{bmatrix}\sigma^2_{pe_{stress}} & \sigma_{pe_{stress},pe_{no\_stress}}\\ \sigma_{pe_{stress},pe_{no\_stress}} & \sigma^2_{pe_{no\_stress}}\end{bmatrix},$$

$$\text{var}\begin{bmatrix}\mathbf{s}_{stress}\\ \mathbf{s}_{no\_stress}\end{bmatrix} = \mathbf{R}\otimes\mathbf{I}, \text{ in which } \mathbf{R} = \begin{bmatrix}\sigma^2_{s_{stress}} & \sigma_{s_{stress},s_{no\_stress}}\\ \sigma_{s_{stress},s_{no\_stress}} & \sigma^2_{s_{no\_stress}}\end{bmatrix},$$

and

$$\text{var}\begin{bmatrix}\mathbf{e}_{stress}\\ \mathbf{e}_{no\_stress}\end{bmatrix} = \mathbf{R}\otimes\mathbf{I}, \text{ in which } \mathbf{R} = \begin{bmatrix}\sigma^2_{e_{stress}} & \sigma_{e_{stress},e_{no\_stress}}\\ \sigma_{e_{stress},e_{no\_stress}} & \sigma^2_{e_{no\_stress}}\end{bmatrix}.$$

RESULTS

Reproductive and Environmental Data

On average, 87% of the sows farrowed after the first insemination. Almost 43% of the observations at 21 d before first insemination had a maximum ambient temperature greater than 19.2°C. Sows were exposed to considerably different ambient temperatures; the maximum ambient temperature recorded was 40.7°C. As shown in Fig. 2, seasonal variation in FR exists beyond the effect of ambient temperature. A decline in FR was observed when first insemination took place around late summer to early autumn.

To identify when, exactly, sows recognize changes in photoperiod, we analyzed the effect of shifting the inflection point of photoperiod 30 d before and 30 d after March 21. The effect of change in photoperiod for each date when shifting the inflection point of photoperiod 30 d before and 30 d after March 21 are shown in Fig. 3. Change in photoperiod had its greatest effect on FR when the inflection point of photoperiod is set at March 13. Almost 50% of the observations had a change in photoperiod lower than 0 at day of first insemination. Further models were run considering the inflection point of photoperiod at March 13. From the base linear model, we observed that the average FR dropped when photoperiod decreased after many days of long photoperiods and FR raised when photoperiod increased after many days of short photoperiods (Fig. 4A) and FR dropped with increasing ambient temperature (Fig. 4B). On average, the FR dropped 2% at the start of autumn with cosine-function values of −1.0 compared with the start of summer with cosine-function values of 0 and dropped 0.2% per increased degree Celsius above 19.2°C.

Comparison of Reaction Norm Models

For reaction norm models, including a slope on change in photoperiod (models RN_1 and RN_2) substantially improved the goodness-of-fit compared with the base model (model M_1). Including both slopes (models RN_3 and RN_4), the slope on change in photoperiod and the slope on ambient temperature, further improved the goodness-of-fit compared with the reaction norm model with only a slope on change in photoperiod (models RN_1 and RN_2; Table 2), The improvement of the goodness-of-fit if grouping of heterogeneity of residual variance was performed based

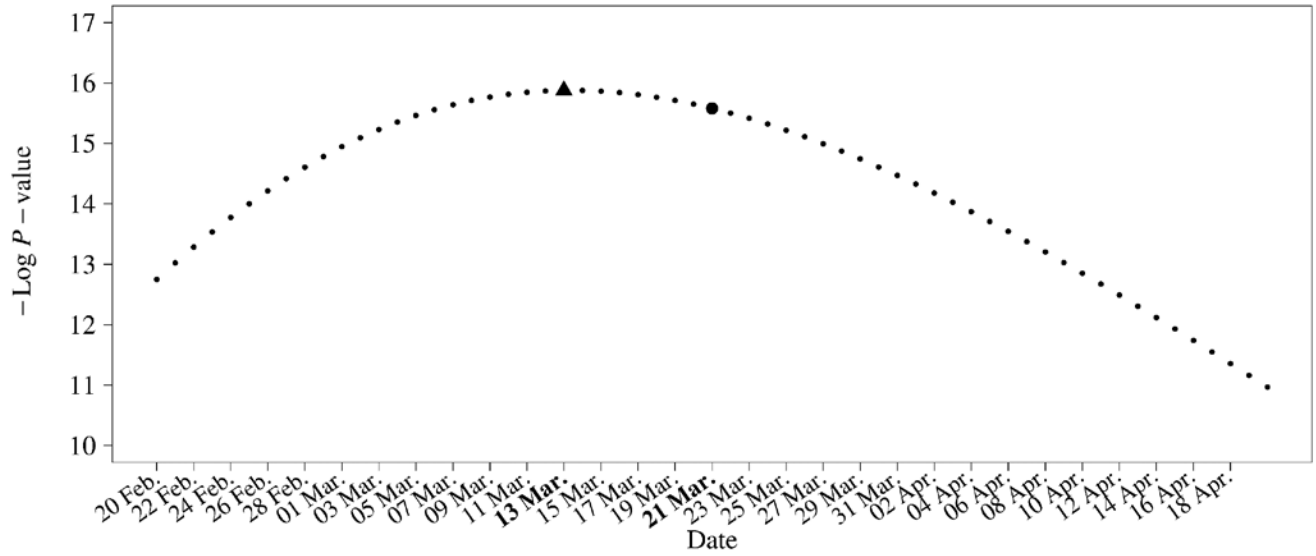

Figure 3. Significance of the effect of change in photoperiod on farrowing rate when shifting the inflection point of photoperiod 30 d before and 30 d after March 21 (●). On the *y* axis are −log10 of *P*-values. On the *x* axis are the dates corresponding to 30 d before and 30 d after March 21. The triangle (▲) shows the most significant date.

on ambient temperature or based on change in photoperiod. Grouping of heterogeneity of residual variance based on ambient temperature better fitted the data than grouping based on change in photoperiod (RN_1 vs. RN_2 and RN_3 vs. RN_4). The best fitting model was RN_3, a reaction norm model including both the slope on change in photoperiod and the slope on ambient temperature and with grouping heterogeneity of residual variance based on ambient temperature.

Genetic Variance in Response to Change in Photoperiod and Ambient Temperature

Estimated variance components for FR using the reaction norm models RN_3 and RN_4 are shown in Table 3. The additive genetic variance of intercept was 23.88 when grouping of heterogeneity of residual variance was based on ambient temperature (RN_3) and 15.03 when grouping was based on change in photoperiod (RN_4). The additive genetic variance of intercept represents the additive genetic variance in performance in a neutral environment, that is, change in photoperiod around 0 and no heat stress (≤19.2°C). The additive genetic variances of the slopes on change in photoperiod and ambient temperature represent the genetic variance in responses of pigs to gradual changes in photoperiod and ambient temperature, respectively. In general, additive genetic variance increases at environments with larger negative changes in photoperiod or environments with higher temperatures. At a change in photoperiod of −1, additive genetic variance was 36.2 for RN_3 and 29.3 for RN_4. At an ambient temperature of 30°C, additive genetic variance for ambient temperature was 91.0 for RN_3 and 137.6 for RN_4. The permanent environmental variance was as large as 14.36 for RN_3 and 11.53 for RN_4. The variance explained by the sire was large, around 25.5 for both models.

Estimates of genetic correlations between FR when there is no change in photoperiod and FR at different classes of changes in photoperiod using models RN_3 and RN_4 are shown in Fig. 5A. The genetic correlations between FR at the UCT of 19.2°C and FR at different ambient temperature classes calculated using the same models are shown in Fig. 5B. Both reaction norm models estimated similar genetic correlations between intercept and changes in photoperiod or between intercept and ambient temperature; however, RN_3 better fitted the data than RN_4, as showed in the model comparison section (Table 2). Therefore, in the next part we present results of only RN_3.

Reaction Norms for Change in Photoperiod and Ambient Temperature

Genetic correlations among intercept, slope of change in photoperiod, and slope of ambient temperature for the reaction norm model with residuals grouped based on ambient temperature (RN_3) are shown in Table 3. The genetic correlation between intercept and slopes of change in photoperiod or ambient temperature represents how the response of pigs to gradual change in photoperiod or ambient temperature could be modified if selection is performed at intercept, that is, around zero change in photoperiod and no heat stress (≤19.2°C). The genetic correlation between intercept and change in photoperiod slope was negative (−0.59 ± 0.1). The genetic correlation between the intercept and ambient temperature slope was also negative but weaker (−0.28 ± 0.1). The negative correlation means that pigs with a high FR at a neutral environment, that is, the intercept, will show

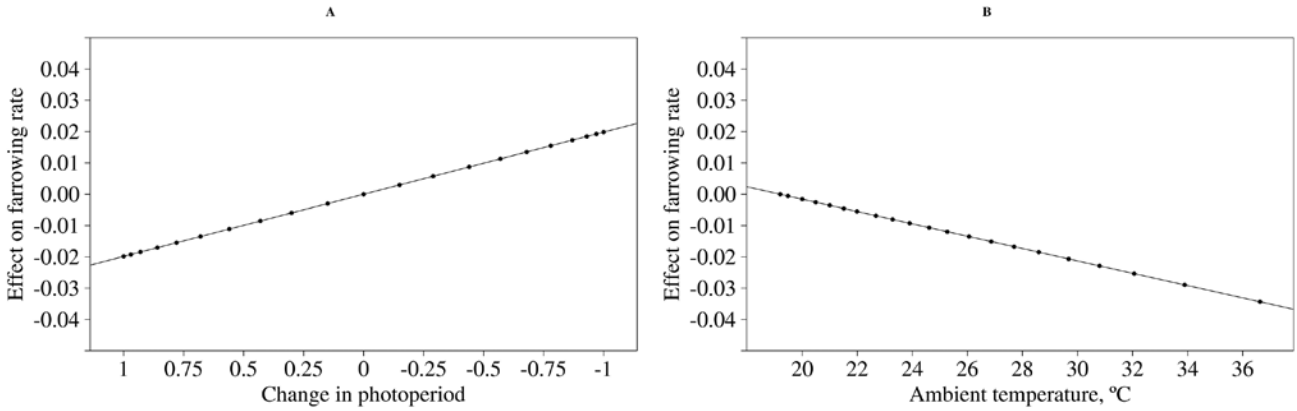

Figure 4. Effect of change in photoperiod on farrowing rate (A) and effect of ambient temperature on farrowing rate (B), estimated using the base linear model number 1 (M_1).

a higher decrease in FR with decreasing daily photoperiod or with higher ambient temperatures. Figure 6A shows variation among pigs for estimated breeding values for FR across different changes in photoperiods. The pigs with high FR in positive environments (increasing daily photoperiod) showed larger reductions in FR with changes in photoperiod toward −1 than pigs with lower FR in neutral environments. Figure 6B shows variation among pigs for estimated breeding values for FR estimates across different ambient temperatures. The pigs with high FR in neutral environments (ambient temperature ≤ 19.2°C) showed larger reductions in FR with increasing ambient temperatures than pigs with lower FR in neutral environments. Both environmental stressors, change in photoperiod and ambient temperature, produced reranking of pigs; more extreme reranking was observed with ambient temperature because the genetic correlation between the intercept and ambient temperature slope was lower than the correlation between the intercept and change in photoperiod slope. The genetic correlation between the slope of change in photoperiod and the slope of ambient temperature was positive (0.68 ± 0.1), indicating that response to change in photoperiod and ambient temperature are genetically correlated, so they can be improved together.

Table 3. Estimated variance components for reaction norm model numbers 3 and 4 (RN_3 and RN_4). Standard errors are in parentheses.

Variance components	RN_3	RN_4
Additive genetic variance		
Intercept (int)	23.88 (4.2)	15.03 (3.6)
Change in photoperiod slope (ph)	36.22 (5.7)	29.28 (5.3)
Ambient temperature slope (t)	0.78 (0.2)	1.18 (0.2)
Corr(int, t)	−0.28 (0.1)	0.09 (0.2)
Corr(int, ph)	−0.59(0.1)	−0.14 (0.1)
Corr(t, ph)	0.68 (0.1)	0.59(0.1)
Permanent environmental variance	14.36 (4.1)	11.53 (4.1)
Service sire variance	25.89 (2.5)	25.28(2.5)

Genotype by Environment Interaction

The additive genetic variances and heritability estimates for FR in each of the 5 environmental classes will be presented only for the reaction norm model with residual grouping performed based on ambient temperature (RN_3). Additive genetic variances and heritability estimates for FR in each of the 5 environmental classes are shown in Table 4. The grouping goes from nonstress environments (class 1) to severe stress environments (class 5). Both additive genetic variance due to change in photoperiod and additive genetic variance due to ambient temperature increased from nonstress environments (class 1) to severe stress environments (class 5). The increase in the additive genetic variance due to increased ambient temperature was larger compared with the increase due to decreasing photoperiod. The total additive genetic variance represents the additive genetic variation of FR at neutral environments plus the additive genetic variation for response to change in photoperiod together to response to increments of ambient temperature including the covariances between their additive genetic effects. The total additive genetic variance of FR at severe stress environment (class 5) was almost 7 times greater than the total additive genetic variance at nonstress environment (class 1). The increase in total additive genetic variance of FR was larger than the increase in residual variance from environmental class 1 to environmental class 5. This resulted in higher heritability estimates in environments with larger environmental stress. Heritability estimates were 0.02 at nonstress environments (class 1) and 0.08 at severe stress environments (class 5). Genetic correlations between the neutral environments (i.e., intercept) and each of the 5 environmental classes are shown in Fig. 7. Genetic correlations decreased from nonstress environments to severe stress environments. The genetic correlation between neutral environment and class 1, 2, and 3 were high (≥0.90), indicating that environments with changes in photoperiod greater than −0.4 and ambient temperatures less than 23°C are not stressful enough

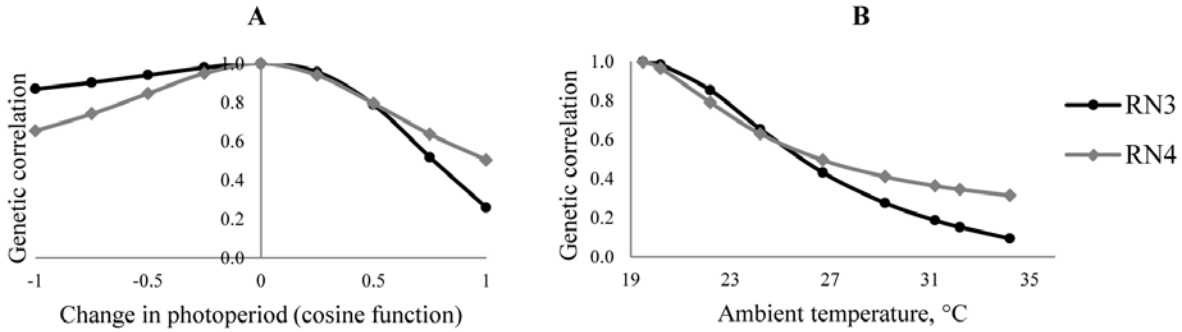

Figure 5. Genetic correlation between farrowing rate (FR) at change in photoperiod equal to 0 and other changes in photoperiod, based on reaction norm model number 3 (RN_3) and reaction norm model number 4 (RN_4; A). Genetic correlation between FR at ambient temperature equal to 19.2°C and other ambient temperatures, based on model RN_3 and model RN_4 (B).

to display differences in ranking of pigs. However, the genetic correlation between intercept and class 5 was as low as 0.46 ± 0.13, indicating substantial reranking of pigs between neutral and severe stress environments.

To check whether the rerankings observed with the reaction norm model were not artifacts of random regression, we estimated variance components with the bivariate model for FR at 2 different environments; the results are shown in Table 5. A nonstressful environment is an environment with ambient temperature lower than or equal to 19.2°C and increasing photoperiod higher than 0.3. A stressful environment is an environment with ambient temperature higher than 22.2°C and decreasing photoperiod lower than −0.3. Similar to the estimates obtained with the reaction norm model, the genetic analysis of FR at opposite environments with a bivariate model also indicated substantial reranking of pigs between nonstressful and stressful environments. The additive genetic variance was 2 times higher at a stressful environment than at a nonstressful environment, and the genetic correlation between FR at both environments was 0.76. The service sire variance was 2 times higher at a stressful environment than at a nonstressful environment, and the correlation for service sire between FR in both environments was little correlated (0.38). The permanent environmental variance was slightly larger at a stressful environment than at a nonstressful environment, and the permanent environment between FR in both environments was totally correlated (0.99). Heritability estimates were 0.02 at a nonstressful environment and 0.03 at a stressful environment.

DISCUSSION

In this study, our main aims were to estimate the additive genetic variation among pigs for FR in response to change in photoperiod and to estimate the genetic correlation between response of pigs to change in photoperiod and response to ambient temperature using a reaction norm model.

Effect of Changes in Photoperiod on Farrowing Rate

A drop in performance during late summer and early autumn was observed in our data for FR even after correction for high ambient temperatures. Despite the protection against changes in photoperiod and ambient temperature variation due to confined conditions, a seasonal infertility remains noticeable at commercial pig farms. Changes in photoperiod and ambient temperature act at different times, yet some overlapping occurs and might produce a synergic effect affecting sows' fertility during late summer and early autumn. When changes in photoperiod and ambient temperature were included in the model to predict FR (M_1), both had a significant effect on FR. Moreover, photoperiod can dependent on latitude, and including latitude of the farm location to characterize the amplitude of the cosine function might have resulted in a better representation of photoperiod. However, latitude confounds with ambient temperature; therefore, including both covariables in the model is not useful.

The role of annual variation in photoperiod to control the neuroendocrine mechanisms involved in season fertility was described for sows by Tast et al. (2000) and more extensively for ewes by Rosa and Bryant (2003). Long photoperiods decrease the secretion of melatonin in sows, which is inhibitory for GnRH secretion (Tast et al., 2000). The exact mechanism of photoperiod on melatonin, however, is not well documented, but it seems that pattern and duration of melatonin secretion is important to synchronize the timing of the breeding season (Tast et al., 2000). And there is no attenuation in the photoperiodic melatonin transduction in the domestic pig due to altered light environment (Tast et al., 2001). In line with this, days longer than 12 h are observed in the Northern Hemisphere between March 21 (start spring) and September 21 (start autumn), and seasonal infertility is observed during late summer and early autumn. Therefore, long days start earlier than a drop in production is observed (Almond, 1992; Tast et al., 2001). This substantiates the need of the sow to recognize a photoperiod pattern to affect FR. Therefore, change in photoperiod modeled using the cosine function well describes

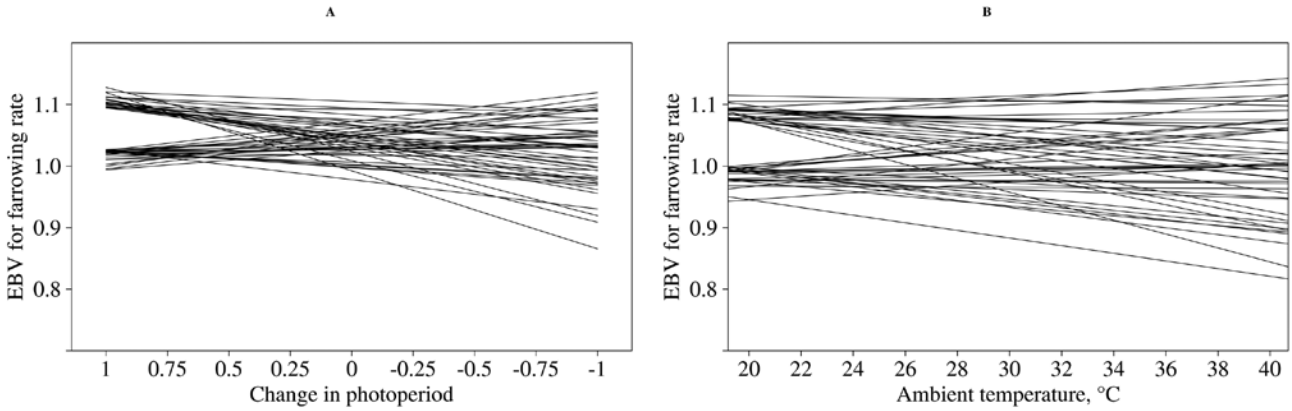

Figure 6. Reaction norms of estimated breeding values for farrowing rate with changing daily photoperiod (A) or increasing ambient temperature (B), using reaction norm model number 3 (RN_3). The breeding values were sampled from 25 pigs with the highest breeding value at a neutral environment and 25 pigs with the lowest breeding value at a neutral environment for farrowing rate.

the response of sows to photoperiod. With this model, the lowest FR is expected when first inseminations are performed around mid September, when function values of change in photoperiod are −1.0 and sows experienced a decreased in photoperiod after many days on long photoperiods. This study was done with data coming from controlled pig farms, and we that observed the negative effect of decreasing photoperiod and high ambient temperature on FR was significant; we expect that the relevance of the results from this study can be even higher for outdoor pig farms, where changes in photoperiod and ambient temperature variation are not mitigated by a controlled environment as in indoor pig farms.

Benefits of the Reaction Norm Model

This is the first time, to our knowledge, that variation in livestock performance is analyzed using a reaction norm with 2 climatic factors. We used a reaction norm model to estimate genetic variation among pigs in response to change in photoperiod and ambient temperature. Reaction norm models are able to capture

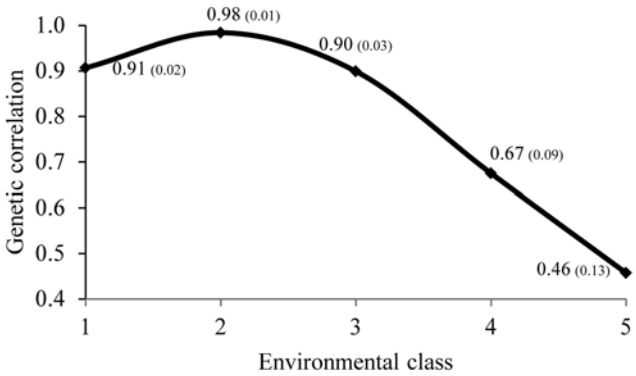

Figure 7. Genetic correlation between farrowing rate at intercept and the 5 environmental classes, based on reaction norm model number 3 (RN_3). Standard errors are in parentheses. Intercept (change in photoperiod [PH] = 0 and ambient temperature [T] ≤ 19.2°C), class 1 (PH = 0.35 and T = 10.45°C), class 2 (PH = −0.28 and T = 20.47°C), class 3 (PH = −0.39 and T = 23.25°C), class 4 (PH = −0.50 and T = 26.91°C), and class 5 (PH = −0.86 and T = 36.60°C).

animal tolerance to environmental stress (Schaeffer, 2004). A reaction norm model takes advantage of individual repeated observations along the continuity of the environmental parameter, in our case, change in photoperiod and ambient temperature. Environmental parameters such as ambient temperature, humidity index, and disease load have been studied mainly in farm animals. Rashidi et al. (2014) and Mathur et al. (2014) studied the variation among sows in response to porcine reproduction and respiratory syndrome and showed the usefulness of reaction norm models as an approach for selection of sows to increase disease resistance and tolerance and that a reaction norm model has a better predictive ability compared with a conventional univariate model and a bivariate model. However, in both studies, they derived the environmental parameter using average estimates of reproduction records. In other studies, the environmental parameter is directly available without the need to derive it from the same data, that is, ambient temperature.

When using directly available environmental parameters, the advantage is that the environmental parameters are easy to interpret and do not depend on the data, which is the case with derived parameters, such as herd–year–season or challenge loads effects. Brügemann et al. (2013), for instance, showed the application of reaction norm animal models to study additive genetic effects of binary traits, such as conception rate and somatic cell score of dairy cows, in response to a temperature–humidity index. Similarly, in pigs, Bloemhof et al. (2012) used ambient temperature as the covariate to estimate reaction norms of FR on ambient temperature. In the last 2 mentioned studies, the reaction norm model was able to capture additive genetic variation in response to heat stress.

In our study, besides ambient temperature, we used change in photoperiod as a covariate in reaction norm because of its continuous nature. We showed that including the slopes of change in photoperiod and

Table 4. Estimated additive genetic variance for change in photoperiod slope ($\sigma^2_{a_{ph}}$) and ambient temperature slope ($\sigma^2_{a_t}$), total genetic variance ($\sigma^2_{a_{\text{total}}}$), residual variance ($\sigma^2_e$), and heritability ($h^2$) for farrowing rate for each of the 5 environmental classes of reaction norm model number 3 (RN_3). Standard errors are in parentheses

Class	$\sigma^2_{a_{ph}}$ [1]	$\sigma^2_{a_t}$ [2]	$\sigma^2_{a_{\text{total}}}$ [3]	σ^2_e	h^2
1	4.44 (0.7)	0.00	16.02 (3.6)	884.95 (7.8)	0.02 (<0.01)
2	2.84 (0.4)	1.26 (0.3)	32.18 (4.8)	881.49 (17.0)	0.03 (0.01)
3	5.51 (0.9)	12.82 (2.6)	34.68 (4.9)	992.41 (18.9)	0.03 (<0.01)
4	9.06 (1.4)	46.44 (9.6)	50.36 (7.4)	999.47 (19.4)	0.05 (0.01)
5	26.79 (4.2)	140.29 (29.0)	105.10 (17.1)	1,107.04 (25.3)	0.08 (0.01)

[1]Additive genetic variance due to only change in photoperiod.

[2]Additive genetic variance due to only ambient temperature.

[3]Additive genetic variance due to change in photoperiod and ambient temperature together including the covariances between their additive genetic effects.

the slope of ambient temperature in a reaction norm model improved the goodness-of-fit for FR compared with a linear model. Most of the sows had more than 1 observation, which enabled the estimation of the 2 slopes. This model was successful in disentangling additive genetic variation due to environmental factors in 2 components, additive genetic variation in response to change in photoperiod and additive genetic variation in response to ambient temperature.

Genetic Correlation between Intercept and Slopes of the Reaction Norms

With the genetic parameters estimated with the reaction norm model, we were also able to estimate genetic correlations among intercept, slope of change in photoperiod, and slope of ambient temperature. Genetic correlation between intercept and slopes depends on where the intercept is positioned (Van Tienderen and Koelewijn, 1994). When only 1 environmental covariate is used for the slope of the reaction norm, you could cautiously set the intercept at the mean environment at natural conditions. However, when 2 environmental covariates are used for the slopes of the reaction norm, the position of the intercept is set where both covariates are 0. Van Tienderen and Koelewijn (1994) showed that the correlations between intercept and slope can shift from −1 to 1 depending on where the intercept is positioned. The interpretation of results, therefore, has to be done relative to the intercept position used in the model. Moreover, correlations between intercept and slope also can shift depending on the way the data is grouped to consider heterogeneity of residual variance; this can be observed in the different estimates we obtained with the reaction norm model with classes for residual variance based on ambient temperature compared with the reaction norm model with classes for residual variance based on change in photoperiod. In our analysis, a reaction norm model with grouping of residual variance based on ambient temperature, the negative genetic correlation obtained between the intercept and change in photoperiod slope indicates that sows with high FR at this intercept are less tolerant to change in photoperiod (Fig. 6A). Evaluation for long-days tolerance, therefore, will benefit from inseminations performed at decreasing photoperiods after many days of long photoperiods to better realize the potential of pigs to cope with this type of environment. Similarly, negative genetic correlation obtained between intercept and ambient temperature slope indicates that the sows with high FR at environments with ambient temperatures ≤ 19.2°C are also less tolerant to high ambient temperature (Fig. 6B). Therefore, genetic selection for heat tolerance should be conducted using data from environments with high ambient temperature to better realize the potential of pigs to cope with this type of environmental stress. The genetic correlation between intercept and ambient temperature slope also depends on the UCT, as this forms the basis for no heat stress. Bloemhof et al. (2012) used the same UCT and dam lines as used in this study and reported a negative genetic correlation (−0.36) between intercept and ambient temperature slope for the International Large White dam line and a positive correlation (0.16) between intercept and slope on ambient temperature for the Dutch Large White dam line, which are in the range of what we obtained, −0.28 with RN_3 and 0.09 with RN_4, although we estimated with both lines together. Zumbach et al. (2008) reported a negative correlation between the intercept and the slope on a temperature–humidity index for finisher pigs, using an UCT of 18°C, again showing the importance of knowing the intercept for interpretation of results. This study shows that interpretation of results from reaction norm models should be done in terms of the position of the intercept, especially when 2 slopes are used, because with 2 slopes, the intercept is when both covariates are 0, whereas with 1 slope, the intercept is where 1 covariate is 0. The large variance of the slopes for change in photoperiod and ambient temperature, and the observed reranking of pigs, shows that selecting for higher FR at neutral environment is genetically related to environmental sensitivity to decreasing daily photoperiod and

Table 5. Estimated variance components of the bivariate model farrowing rate at nonstressful environment (FR_{no_stress}) and for farrowing rate at stressful environment (FR_{stress}). Standard errors are in parentheses.

Variance components	FR_{no_stress}	FR_{stress}
Additive genetic	14.70 (5.2)	33.36 (10.3)
Permanent environmental variance	22.30 (4.1)	26.12 (14.8)
Service sire variance	27.40 (4.0)	53.53 (8.6)
Heritability	0.02 (0.01)	0.03 (0.01)
Genetic corr(stress, no_stress)[1]	0.76 (0.19)	
Perm corr(stress, no_stress)[2]	0.99 (0.50)	
SSire corr(stress, no_stress)[3]	0.38 (0.12)	

[1]Correlation between additive genetic effect on performance in stressful environments (stress) and nonstressful environments (no_stress).

[2]Correlation between effect of permanent environment (Perm corr) on performance in stressful environments (stress and nonstressful environments (no_ stress).

[3]Correlation between effect of service sire (Ssire corr) on performance in stressful environments (stress and nonstressful environments (no_stress).

higher ambient temperatures. Furthermore, response on change in photoperiod and response to ambient temperature are positively correlated, meaning that pigs tolerant to long days are also tolerant to heat stress and that selection for long-days tolerance comes as a by-product of selection for heat tolerance or vice versa.

Genetic Variation in Pigs for Farrowing Rate in Different Environments

Due to the existence of additive genetic variation in response to change in both photoperiod and ambient temperature, additive genetic variance increased in stressful environments. Even when heterogeneity of residual variances was considered to avoid individual variances to increase as a function of increased environmental stress (Lillehammer et al., 2009), the residual variance increased in stressful environments resulting in substantial higher phenotypic variance in these environments. Stressful conditions, such as decreasing daily photoperiod and high ambient temperatures, increase individual differences in performance (Charmantier and Garant, 2005). The increased heritability of FR at more stressful environmental classes was mainly due to an increase of additive variance, because the increase of residual variance was not large enough to conceal the increase of the heritability. We analyzed our data also with a bivariate model to prove that the reaction norm model estimates were not an artifact. With the bivariate model, we also observed that additive genetic variation among pigs for FR performance is larger at environments with decreasing daily photoperiod and high ambient temperature. However, with a bivariate model, we cannot take advantage of the continuous nature of the covariates change in photoperiod and ambient temperature.

Genetic correlations between FR in nonstressful environments and stressful environments showed that FR is genetically a different trait at the 2 extreme environments, as shown by the 2 types of models used in this study, reaction norm and bivariate. The low genetic correlation between nonstressful environments and stressful environments shows that selection without considering environmental variation is suboptimal for realizing the pigs' potential to maintain performance when decreasing daily photoperiods or with high ambient temperatures. The presence of G×E highlights the fact that the genetics that are suitable for environments with temperate climates are different from the genetics that are suitable for challenged environments (Silva et al., 2014). Besides, we also estimated a large variance due to service sire, and with the bivariate model, we observed that the service sire variance increased at stressful environments; a similar analysis will be interesting to perform to estimate if there is additive genetic variation among boars for response to changes in photoperiod. It has been shown that semen production and semen quality is negatively affected by decreasing daily photoperiod (Andersson et al., 1998; Sancho et al., 2004). In this sense, if genetic variation for tolerance to long days exists among boars, semen production of tolerant boars can be used during environmentally stressful periods or in countries with environmentally stressful conditions.

In general, if pigs are aimed to perform at challenging climates, for example, Nordic countries with large changes in photoperiods or tropical countries with very high ambient temperatures, breeding values of these pigs should be estimated for the specific combination of change in photoperiod and ambient temperature using the genetic parameters estimated in this study. In the selection index for pure lines, some emphasis may be placed on FR in stressful environments. To increase long-days tolerance and heat tolerance, both slopes should be included in the selection index. In addition, dams used for making crossbred F_1 sows in challenged environments could be sorted on their breeding values for FR during decreasing daily photoperiods or at high temperature.

Conclusion

Our study shows that there is significant genetic variation for FR in response to change in photoperiod and ambient temperature. Genetic variation for FR is larger in environments with decreasing daily photoperiod and high ambient temperatures compared with neutral environments. Reaction norm models are quite useful to study variation among pigs under different environmental conditions. Therefore, selection of pigs for long-days tolerance and heat tolerance is possible. It should be conducted using records collected in the

presence of environmental stressors, where there is a better expression of genetic potential of pigs. The genetic correlation between response to change in photoperiod and response to ambient temperature is positive, indicating that selection for long-days tolerance should also improve heat tolerance or vice versa.

LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: Proc. 2nd Int. Symp. Inf. Theory, Akademiai Kiado, Budapest, Hungary. p. 267–281.

Almond, G. 1992. Seasonal infertility in female pigs. In: Vol. 1, Proc. North Carolina Healthy Hog Semin., Raleigh, NC. p. 1–5.

Almond, P. K., and G. Bilkei. 2005. Seasonal infertility in large pig production units in an Eastern-European climate. Aust. Vet. J. 83:344–346. doi:10.1111/j.1751-0813.2005.tb15627.x

Andersson, H., M. Wallgren, L. Rydhmer, K. Lundström, K. Andersson, and M. Forsberg. 1998. Photoperiodic effects on pubertal maturation of spermatogenesis, pituitary responsiveness to exogenous GnRH, and expression of boar taint in crossbred boars. Anim. Reprod. Sci. 54:121–137. doi:10.1016/S0378-4320(98)00149-3

Anil, S. S., A. Larriestra, J. Deen, and L. Anil. 2005. A path analysis of the factors associated with seasonal variation of breeding failure in sows. Can. J. Anim. Sci. 85:317–325. doi:10.4141/A05-006

Auvigne, V., P. Leneveu, C. Jehannin, O. Peltoniemi, and E. Sallé. 2010. Seasonal infertility in sows: A five year field study to analyze the relative roles of heat stress and photoperiod. Theriogenology 74:60–66. doi:10.1016/j.theriogenology.2009.12.019

Bergsma, R., and S. Hermesch. 2012. Exploring breeding opportunities for reduced thermal sensitivity of feed intake in the lactating sow. J. Anim. Sci. 90: 85-98. doi:10.2527/jas.2011-4021

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. J. Anim. Sci. 90:2109–2119. doi:10.2527/jas.2011-4650

Bloemhof, S., P. K. Mathur, E. F. Knol, and E. H. van der Waaij. 2013. Effect of daily environmental ambient temperature on farrowing rate and total born in dam line sows. J. Anim. Sci. 91:2667–2679. doi:10.2527/jas.2012-5902

Bloemhof, S., E. H. van der Waaij, J. W. M. Merks, and E. F. Knol. 2008. Sow line differences in heat stress tolerance expressed in reproductive performance traits. J. Anim. Sci. 86:3330–3337. doi:10.2527/jas.2008-0862

Brügemann, K., E. Gernand, U. U. von Borstel, and S. König. 2013. Application of reaction norm models to infer the genetic background and phenotypic trajectory of binary conception rate by alterations of temperature × humidity indices. Livest. Sci. 157:389–396. doi:10.1016/j.livsci.2013.08.009

Charmantier, A., and D. Garant. 2005. Environmental quality and evolutionary potential: Lessons from wild populations. Proc. R. Soc. B 272:1415–1425. doi:10.1098/rspb.2005.3117

Chokoe, T. C., and F. K. Siebrits. 2009. Effects of season and regulated photoperiod on the reproductive performance of sows. S. Afr. J. Anim. Sci. 39:45–54. doi:10.4314/sajas.v39i1.43545

Freitas, M. S., I. Misztal, J. Bohmanova, and J. West. 2006. Utility of on- and off-farm weather records for studies in genetics of heat tolerance. Livest. Sci. 105:223–228. doi:10.1016/j.livsci.2006.06.011

Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2009 ASReml user guide release 3.0. http://www.vsni.co.uk. (Accessed 12 May 2015.)

Hälli, O., A. Tast, M. Heinonen, C. Munsterhjelm, A. Valros, and O. A. T. Peltoniemi. 2008. Short or long day light regimes may not affect reproductive performance in the sow. Reprod. Domestic. Anim. 43:708-712. doi: 10.1111/j.1439-0531.2007.00976.x

Koninklijk Nederlands Meteorologisch Instituut (KNMI). 2015. Daggegevens van het weer in Nederland. http://www.knmi.nl/nederland-nu/klimatologie/daggegevens. (Accessed 12 May 2015.)

LeMoine, A. 2013. Meteorological effects on seasonal infertility in pigs. PhD Diss. University of Leeds, Leeds.

Lillehammer, M., J. Ødegård, and T. Meuwissen. 2009. Reducing the bias of estimates of genotype by environment interactions in reaction norm sire models. Genet. Sel. Evol. 41:30. doi:10.1186/1297-9686-41-30

Mathur, P. K., J. M. Herrero-Medrano, P. Alexandri, E. F. Knol, J. T. Napel, H. Rashidi, and H. A. Mulder. 2014. Estimating challenge load due to disease outbreaks and other challenges using reproduction records of sows. J. Anim. Sci. 92:5374–5381. doi:10.2527/jas.2014-8059

National Climatic Data Center (NCDC). 2015. NNDC climate data online. http://www7.ncdc.noaa.gov/CDO/cdoselect.cmd?datasetabbv=GSOD&countryabbv=&georegionabbv=. (Accessed 12 May 2015.)

Peltoniemi, O. A. T., R. J. Love, M. Heinonen, V. Tuovinen, and H. Saloniemi. 1999. Seasonal and management effects on fertility of the sow: A descriptive study. Anim. Reprod. Sci. 55:47–61. doi:10.1016/S0378-4320(98)00159-6

Rashidi, H., H. A. Mulder, P. Mathur, J. A. M. van Arendonk, and E. F. Knol. 2014. Variation among sows in response to porcine reproductive and respiratory syndrome. J. Anim. Sci. 92:95–105. doi:10.2527/jas.2013-6889

Rosa, H. J. D., and M. J. Bryant. 2003. Seasonality of reproduction in sheep. Small Rumin. Res. 48:155–171. doi:10.1016/S0921-4488(03)00038-5

Sancho, S., E. Pinart, M. Briz, N. Garcia-Gil, E. Badia, J. Bassols, E. Kádár, A. Pruneda, E. Bussalleu, M. Yeste, M. G. Coll, and S. Bonet. 2004. Semen quality of postpubertal boars during increasing and decreasing natural photoperiods. Theriogenology 62:1271–1282. doi:10.1016/j.theriogenology.2004.01.003

Schaeffer, L. R. 2004. Application of reaction norm models in animal breeding. Livest. Prod. Sci. 86:35–45. doi:10.1016/S0301-6226(03)00151-9

Silva, F. F., H. A. Mulder, E. F. Knol, M. S. Lopes, S. E. F. Guimarães, P. S. Lopes, P. K. Mathur, J. M. S. Viana, and J. W. M. Bastiaansen. 2014. Sire evaluation for total number born in pigs using a genomic reaction norms approach. J. Anim. Sci. 92:3825–3834. doi:10.2527/jas.2013-6486

Tast, A., O. Halli, S. Ahlstrom, H. Andersson, R. J. Love, and O. A. T. Peltoniemi. 2001. Seasonal alterations in circadian melatonin rhythms of the European wild boar and domestic gilt. J. Pineal Res. 30:43–49. doi:10.1034/j.1600-079X.2001.300106.x

Tast, A., R. J. Love, I. J. Clarke, and G. Evans. 2000. Effects of active and passive gonadotrophin-releasing hormone immunization on recognition and establishment of pregnancy in pigs. Reprod. Fertil. Dev. 12:277–282. doi:10.1071/RD00063

Tast, A., O. A. T. Peltoniemi, J. V. Virolainen, and R. J. Love. 2002. Early disruption of pregnancy as a manifestation of seasonal infertility in pigs. Anim. Reprod. Sci. 74:75–86. doi:10.1016/S0378-4320(02)00167-7

Van Tienderen, P. H., and H. P. Koelewijn. 1994. Selection on reaction norms, genetic correlations and constraints. Genet. Res. 64:115–125. doi:10.1017/S0016672300032729

Zumbach, B., I. Misztal, S. Tsuruta, J. P. Sanchez, M. Azain, W. Herring, J. Holl, T. Long, and M. Culbertson. 2008. Genetic components of heat stress in finishing pigs: Parameter estimation. J. Anim. Sci. 86:2076–2081. doi:10.2527/jas.2007-0282