ABSTRACT: The aims of this study were, first, to evaluate the effects of climatic variables on daily feed intake of lactating sows and, second, to establish whether the response of sows to variation in temperature on feed intake during lactation was heritable. A total of 82,614 records for daily feed intake during lactation were available for 848 sows with 3,369 litters farrowing from January 2000 to December 2007. Climatic parameters available from the nearest weather station were maximum 24 h outside temperature, day length changes, and humidity. Although ambient room temperature was modified at the animal level in the farrowing shed, these climatic variables still had a significant effect on feed intake during lactation. Regression coefficients temperature and humidity were 0.01385 ± 0.00300 (temperature) − 0.00031 ± 0.00009 (temperature²) and 0.01443 ± 0.00620 (humidity) − 0.00009 ± 0.00004 (humidity²). There was an interaction between temperature and humidity, partly due to the climate control in the farrowing shed. At low temperature, feed intake increased considerably with greater humidity, in contrast to a small reduction in feed intake with greater humidity at high temperature. Day length change was modeled with a cosine function. At the start of autumn (September 21), sows ate 0.36 ± 0.056 kg/d less feed than at the start of spring (March 21). Daily feed intake during lactation was described as a function of days in lactation and as a function of both days in lactation and temperature using random regression models. The average heritability and repeatability summarized over the day in lactation at the mean temperature were 0.21 and 0.69, respectively. Genetic variance of temperature response on feed intake was less than 20% of the day effect. The permanent environmental variance was 2-fold (day) and 4-fold (temperature) greater than the corresponding additive genetic variance. Heritabilities of daily feed intake were greater during the first week of lactation compared with the rest of lactation. The genetic correlation between days decreased as time increased down to about 0.2 between the first and last day in lactation. The genetic correlation between feed intake records at the extreme temperatures decreased to about −0.35. It was concluded that random regression models are useful for research and results may be used to develop simpler models that can be implemented in practical breeding programs. An effect of temperature on lactation feed intake was found even in this climate-controlled environment located in a temperate climate zone. Larger effects are expected in more extreme climatic conditions with less temperature-controlled farrowing sheds.

Key words: lactation, random regression, sow feed intake, temperature tolerance

INTRODUCTION

Commercial pig breeding is a global industry. Therefore, it is important to know whether pigs are able to perform in a wide variety of environments that differ in regard to potential stressors. Pig genotypes may differ in their response to changes in the prevailing environment, giving rise to a genotype × environment interaction. Calculations have shown that in the presence of a genotype × environment interaction the selection for...
high productivity in a nonlimiting environment resulted in an increased environmental sensitivity (Kohlmodin et al., 2003).

Environmental conditions may be described on a continuous scale using a range of descriptors, such as temperature, which quantifies climatic and seasonal influences. In these situations, reaction norm models are useful tools for genetic analysis (de Jong, 1995). These models express performance of a genotype as a function of the environment, thereby providing avenues for selection of highly productive animals with low environmental sensitivity.

Lactation is a critical phase for piglets as well as for sows. A high and undisturbed lactation feed intake of the sow ensures a good start of life for piglets and good prospects for the sow for ongoing reproductive success in future parities. However, undisturbed feed intake during lactation is not always achieved. For example, high temperatures have been shown to reduce feed intake in lactating sows (Black et al., 1993; Quiniou and Noblet, 1999). The effect of temperature has to be separated from other climatic and seasonal factors, such as humidity and day length, to quantify the specific response of each genotype to changes in temperature and other climatic factors influencing feed intake of lactating sows. Therefore, the aims of this study were a) to evaluate the effects of climatic variables on daily feed intake of lactating sows and b) to establish whether the response of feed intake of sows during lactation to variation in temperature was heritable.

MATERIALS AND METHODS

Animals were subjected to standard production conditions, and no additional measurements were taken. Consequently, no Care and Use Committee approval was needed. The experimental farm of the Institute of Pig Genetics (IPG), where all observations originated, operates in accordance with the regulations of the Dutch law on protection of animals.

Data Set

The experimental farm of IPG in Beilen (52° 52′ latitude, 06° 31′ longitude, the Netherlands) was used to compare commercial TOPIGS crossbred sows (Vught, the Netherlands) and their offspring based on inseminations with boars from different commercial sire lines. In total, 82,614 daily feed intake observations during lactation were available for 848 sows from 7 line crosses with 3,369 litters, recorded from January 2000 until December 2007. The pedigree file was based on 3 generations of parents and contained 2,963 animals. Observations on feed intake were available for 780 sows with known parentage (losing 68 sows due to lack of pedigree), which descended from 110 sires and 410 dams.

Climatic Data and Climate Control on Farm

Daily temperature (mean, minimum, maximum) and humidity (daily mean relative atmospheric humidity) were available from the nearest weather station in Eelde (53°08′ latitude, 06°35′ longitude) 30 km away from the experimental farm of IPG in Beilen (KNMI, 2010). Day lengths on June 21 and December 21 were 16 h 53 min and 7 h 36 min, respectively. Day light was admitted to each farrowing room via windows. Artificial light was only switched on during animal handling and monitoring. Heat lamps were used only for the first 72 h postfarrowing. From July 2004 onward, ambient room temperature of each farrowing room as well as the outside temperature were recorded each hour at the experimental farm.

Farrowing rooms were ventilated mechanically with inlet air entering the farrowing room via a central corridor where heating elements were located. It was not possible to apply air cooling. At the day of parturition, the target value for the ambient room temperature was 26°C, which was gradually reduced to 25°C at d 18 after farrowing. This target ambient room temperature of 25°C was maintained from d 18 until weaning. The desired farrowing room temperature was adjusted to meet the requirements of piglets and to prevent cold stress in piglets.

A 3-week batch farrowing system was used at the IPG farm consisting of 24 sows, which farrow in 3 farrowing rooms that were equipped with 8 farrowing crates each. The sow that farrowed first in a farrowing room determined the temperature regimen for that farrowing room. The average interval between first and last parturition date was 5.3 d within each farrowing room.

Feeding Schemes

Sows were transferred to the farrowing house on average 8.8 d before parturition. Sows were gradually adapted to a lactation diet, which was fed restrictively applying separate feeding schemes for primiparous and multiparous sows. The feeding scheme represented the maximum amount of feed offered to the sow at each day during lactation (Figure 1a,b). Feed was delivered to each sow twice daily at approximately 0700 and 1500 h by a computerized feeding machine. In an attempt to feed an amount equal to the intake capacity of the sow, the amount of feed for each meal was set by the farm manager daily, and adjusted downward based on the amount of feed not eaten by the sow 2 h after delivery of feed. The daily feed allowance was based upon the feed intake capacity of the sow and was not dependent on the BW of the sow, her body condition, or the number of piglets to be nursed. On average, piglets were weaned at 27.3 d of age. Only the first 28 d of lactation were included in the analyses because the number of observations decreased rapidly after d 28 of
lactation. Feed intake records at the day of parturition (defined as d 0) and at the day of weaning of piglets were excluded.

Net energy content of the commercial lactation diet used at the IPG farm was 9.68 MJ of NE per kilogram feed, which corresponds to 13.5 MJ of ME per kilogram of feed. The feed was supplied in pellets and contained 147.2 g of CP and 8.1 g of lysine per kilogram.

**Statistical Analysis: Fixed Effect Model Selection**

Using inside or outside temperature observations or a combination of both, one can define an almost infinite number of temperature characteristics, such as the maximum or the minimum daily temperature or the largest difference in daily temperature and use these characteristics recorded on the actual day of feed intake or on any day shortly before the actual day of feeding. Likewise, deviation from desired ambient room temperature can be based on numerous different temperature characteristics. In a preliminary study, the maximum 24-h temperature on the day of feed intake appeared to explain most of the variation in feed intake in comparison with other possible choices for temperature (results not shown). In addition to the temperature measurement, the type of temperature measurement must be selected: ambient room temperature, outside temperature (on farm or weather station), or deviation from the desired ambient room temperature. In that same preliminary study, the coefficients of determination of the models to explain variation in daily feed intake containing different temperature measurements were almost identical (results not shown). Therefore, maximum 24-h temperature of the nearest weather station was used in all analyses for the present study because inside ambient room temperature measured on farm was only available for a subset of sows that had insufficient data available for genetic analyses. In addition, greater accuracy of measurements can be achieved at weather stations because the equipment is well maintained and regularly calibrated.

The optimal fixed effect model (model 1) describing variation in daily lactation feed intake was determined using PROC MIXED (SAS Inst. Inc., Cary, NC):

\[
\text{DFI}_{ijklmn} = \mu + \text{DAY}_i(\text{FEEDSCHEME}_j) + \text{PARITY}_k + \text{LINE}_l + b_1\text{TOBN} + b_2\text{DL} + b_3\text{DLC} + b_4\text{HM} + b_5\text{HM}^2 + b_6\text{T} + b_7\text{T}^2 + \text{BATCH}_m + \text{SOW}_n + e_{ijklmn},
\]

where \(\text{DFI}_{ijklmn} = \) daily feed intake (kg/d) of sow \(n\); \(\mu\) is the intercept; \(\text{DAY}_i = \) the effect of day \(i\) during lactation (\(i = 1\) to 28); \(\text{FEEDSCHEME}_j = \) the effect of feeding scheme \(j\) (\(j = 0, 1\)) for primiparous vs. multiparous sows; \(\text{PARITY}_k = \) the effect of parity \(k\) of multiparous sow \(n\) combining parity 6 and above (\(k = 1\) to 5); \(\text{LINE}_l = \) the effect of genetic line (= commercial cross) \(l\) of sow \(n\) (\(l = 1\) to 7); \(\text{TOBN} = \) number of piglets to be nursed; \(\text{DL} = \) day length parameter (for explanation, see Day Length Function section below); \(\text{DLC} = \) day length-change parameter (for explanation, see Day Length Function section below); \(\text{HM} = \) relative atmospheric humidity (%); \(\text{T} = \) maximum 24-h outside temperature reported by the nearest weather station; \(\text{BATCH}_m = \) the (random) effect of the \(m\)th 3-wk outside temperature reported by the nearest weather station; \(\text{SOW}_n = \) the (random) effect of the \(n\)th sow (\(n = 1\) to 848); \(e_{ijklmn}\) is the residual effect of sow \(n\) in her \(k\)th parity belonging to line \(l\) on day \(i\) of lactation applying feeding scheme \(j\) within batch \(m\); and \(b_1\) to \(b_7\) are coefficients of linear regression on their independent effects.

The number of suckling piglets affects milk yield of sows, which, according to Revell and Williams (1993), is likely to be an important driver for feed consumption of sows during lactation. Therefore, the number of piglets to be nursed was part of the model.

**Day Length Function**

Day length and temperature are at least partly confounded. Day length can be modeled by taking the (trigonometric function) sine of the day (1 to 365) of...
feed intake within a year, making sure that the peak of the curve is at the start of summer (June 21). Or, as a formula,

$$\text{day length} = \sin\left(\frac{\text{[(DateFeedIntake} - \text{"21MAR1999")/365.25]} \times (2\pi}\right).$$

The first derivative of day length gives the changes in day length at the day of feed intake (hereafter called day length change), which is the cosine of the day length function. The amount of change in day length is largest at the start of spring (March 21) and autumn (September 21). Function value for an increase in day length was 1.0 (March 21), and it was −1.0 for a decrease in day length (September 21; Figure 2).

**Development of Random Regression Models**

The mean feed intake curve derived from the fixed effects outlined in model 1 was fitted for primiparous and multiparous sows, and deviations in daily feed intake from this curve were estimated for batch, additive genetic, and permanent environmental effect of the sow. Sensitivity of sows to temperature was modeled by applying a reaction norm for each animal, representing its EBV for feed intake on values of temperature on the day of feed intake. Models were progressively extended to higher order Legendre polynomials for feed intake on days of lactation (model 2) as well as feed intake on different temperatures on the day of feed intake (model 3).

Several types of orthogonal polynomials are available, but Legendre polynomials have been commonly used in genetic evaluation of repeated records on individuals over time and in analysis of genotype × environment interaction (Schaeffer, 2004). Analyses were performed using ASReml software (Gilmour et al., 2006). To estimate variance components without including sensitivity to temperature, the general mixed model was applied:

$$DFI_{ino} = fixed + \sum_{p=1}^{k_y} \beta_{np}\theta_p(T^*_on) + \sum_{q=0}^{k_{day}} \alpha_{nq}\varphi_q(day_{in}) + \sum_{q=0}^{k_{day}} \delta_{nq}\varphi_q(day_{in}) + \sum_{q=0}^{k_{day}} \gamma_{mnpq}\varphi_q(day_{in}) + \varepsilon_{ino}.$$  

To account for heritable temperature response of feed intake of sows during lactation, the subjoined was added to this general mixed model:

$$\sum_{p=1}^{k_y} \phi_{np}\theta_p(T^*_on) + \sum_{p=1}^{k_T} \chi_{nq}\theta_p(T^*_on).$$

where $DFI_{ino}$ is the feed intake on day $i$ (kg/d) of animal (sow) $n$ at temperature $o$; fixed is the set of fixed effects as selected from model 1; $T^*_on$ is the standardized temperature class $o$ at day of feed intake fitted as a fixed effect omitting an intercept. Temperature was transformed with mean = 0 and SD = 1, forming 55 classes with intervals of 0.1 SD (−2.5 to +2.9). Further, the fixed random regression coefficients for temperature to model the population mean are $\beta_{np}$; $day_{in}$ is the day $i$ of lactation at recording; $\alpha_{nq}$ and $\delta_{nq}$ are the random regression coefficients for the additive genetic effects of animal $n$ on day and temperature, respectively; $\epsilon_{ino}$ and $\gamma_{mnpq}$ are the random regression coefficients for permanent environmental effect of sow $n$ on day and temperature, respectively; $\gamma_{mnpq}$ are the random regression coefficients for the contemporary group of the animal (batch) for batch class $m$; $\theta_p(T^*_on)$ is the $p$th Legendre polynomial on temperature; $\varphi_q(day_{in})$ is the $q$th Legendre polynomial of day $i$ in lactation; $k_{day}$ and $k_T$ are the order of fit of the Legendre polynomials of day and temperature, respectively; and $\varepsilon_{ino}$ is the random residual effect.

The log-likelihood ratio test was used to compare the fit of 2 models with adjacent orders of polynomials. In matrix notation, model 2 and model 3 were

$$y = Xf + Z_Da_D + W_Dpe_D + T_Db_D + e, \text{ and} [2]$$

$$y = Xf + Z_Da_D + Z_Ta_T + W_Dpe_D + W_Tpe_T + T_Db_D + e, \text{ and} [3]$$

where $y$ is the vector of observations; $f$ is the vector of fixed effects selected from model 1; $a$ is the vector of random additive genetic effects; $pe$ is the vector of random nongenetic effects of the permanent environmental effect of the sow; $b$ is the vector of random effects common to sows with feed intake in the same batch; $X$, $Z$, $W$, and $T$ are incidence matrices; and $e$ is the vector of random residuals. The subscripts $D$ and $T$ represent day-dependent and temperature-dependent effects.

The (co)variance matrix belonging to model 2 was assumed to be
Genetics of thermal sensitivity of sow feed intake

The genetic relationships among all individuals. The appropriate dimensions, and the (co)variance matrix belonging to model 3 was

\[
\begin{bmatrix}
    a_D \\
    pe_D \\
    b_D \\
    e
\end{bmatrix}
\begin{bmatrix}
    K_{AD} \otimes A & 0 & 0 & 0 \\
    0 & K_{PED} \otimes I_{PED} & 0 & 0 \\
    0 & 0 & K_{BD} \otimes I_{BD} & 0 \\
    0 & 0 & 0 & R
\end{bmatrix}
\begin{bmatrix}
    a_D \\
    a_T \\
    pe_D \\
    pe_T \\
    b_D \\
    e
\end{bmatrix}
\]

where \( K_{AD}, K_{AT}, K_{PED}, K_{PET}, \) and \( K_{BD} \) are the matrices of coefficients of the covariance function for additive genetic, permanent environment of the sow, and batch effects dependent on day (D) or temperature (T). Matrix R is a diagonal matrix containing residual variances depending on day of feed intake allowing heterogeneous residual variances. There were 19 measurement error categories because residual variances were allowed to differ for each day of the first 15 d of lactation. The residual variances were assumed to be constant for d 16 to 18, 19 to 21, 22 to 24, and 25 to 28 of lactation. The \( I_{PED}, I_{PET}, \) and \( I_{BD} \) are identity matrices of the appropriate dimensions, and \( A \) is a matrix of additive genetic relationships among all individuals. The \( \otimes \) indicates the Kronecker product of matrices.

The formula to calculate an overall genetic correlation between combinations of observations on 2 (different) days and 2 (different) temperature classes was

\[
r_{g,2} = \frac{\text{cov}(y_{ij}, y_{k}) + \text{cov}(T^*_i, T^*_k)}{\sqrt{\text{var}(y_{ij}) + \text{var}(T^*_i)} \times \sqrt{\text{var}(y_{k}) + \text{var}(T^*_k)}}
\]

where \( y_{ij} \) is the \( i \)th day in lactation; and \( T^*_i \) is the (transformed) temperature class \( o \) on day \( i \).

The formula to calculate the heritability and repeatability of the average of \( n \) repeated records in a repeatability model was as follows (extended from K. Meyer, Animal Genetics and Breeding Unit, University of New England, Armidale, Australia, personal communication):

\[
h^2 = \frac{\sigma^2_{AD} + \sigma^2_{AT}}{\sigma^2_{AD} + \sigma^2_{AT} + \sigma^2_{peD} + \sigma^2_{peT} + \sigma^2_b + \sigma^2_e/n}
\]

\[
r^2 = \frac{\sigma^2_{AD} + \sigma^2_{AT} + \sigma^2_{peD} + \sigma^2_{peT} + \sigma^2_b + \sigma^2_e}{\sigma^2_{AD} + \sigma^2_{AT} + \sigma^2_{peD} + \sigma^2_{peT} + \sigma^2_b + \sigma^2_e/n}
\]

where \( \sigma^2_{AD} \) and \( \sigma^2_{AT} \) are the average additive variances over a trajectory of \( n \) observations for the day-dependent and temperature-dependent effect, respectively; \( \sigma^2_{peD} \) and \( \sigma^2_{peT} \) are the average variances attributable to permanent environment for the day-dependent and temperature-dependent effect; respectively; \( \sigma^2_e \) is the average variance attributable to the batch effect, \( \sigma^2_b \) is the average residual variance; and \( n \) is the number of observations (here, the number of days in lactation).

RESULTS

Data Description

Descriptive statistics are given in Table 1. Outside temperature and humidity observations were available for the entire data set, whereas observations on ambient room temperature were only available for a subset of the data set. The average outside temperature was 12.8°C, whereas the average ambient room temperature was 25.2°C. According to Black et al. (1993), the thermo-neutral zone for lactating sows lies between 12 and 22°C. Consequently, sows were kept at ambient room temperatures that exceeded the upper critical temperature. Note, heating was used to compensate for low temperatures, but no air cooling could be applied. Consequently, at high outside temperatures, mechanical ventilation could not prevent the increase in ambient room temperature. The tail of the temperature distribution to the right (higher temperatures) was therefore larger than the tail of the temperature distribution to the left (lower temperatures).

Primiparous sows were fed a maximum of 7 kg of feed per day (Figure 1a), whereas the maximum feed allowance was 8 kg per day for multiparous sows (Figure 1b). From day of parturition, sows were fed according to an ascending scale until they reached the maximum feed allowance at d 17 of lactation for primiparous sows and at d 13 of lactation for multiparous sows. Note, ADFI (kg) plus the equivalent of 1 SD unit (kg) was, in almost all days of lactation, greater than the programmed feeding scheme projection. However, feeding sows a greater amount of feed than the feed allowance occurred only occasionally (less than 3% of daily feed intake records), indicating that the distribution of daily feed intake within a day was skewed with considerable variation in daily feed intake below the mean. The SD of daily feed intake increased as the day of lactation
increased until the plateau of the feeding scheme was reached after 14 d and remained relatively constant afterward.

The observed mean daily feed intake during lactation for maximum outside temperature, recorded daily over 24 h at the nearest weather station, is shown in Figure 3 (panels a and b) for primiparous and multiparous sows, respectively. Despite the climate control in the farrowing room, a slight decrease in ADFI was observed in multiparous sows from 22°C onward, which had more records available than primiparous sows. Therefore, this observed trend in daily feed intake for multiparous sows was more reliable for the greater temperature range. There was no clear association between feed intake and maximum 24 h outside temperature for temperature ranges below 22°C. The maximum 24-h outside temperature recorded at the nearest weather station was 35.4°C, and the lowest maximum 24-h outside temperature was −6.5°C over an 8-yr period (Table 1). However, extreme temperatures are rare in the maritime climate of the Netherlands, and consequently the number of observations on days with extreme maximum 24-h outside temperatures was limited (Figure 3a, 3b).

**Phenotypic Model**

The results of the PROC MIXED procedure applying model 1 are presented in Table 2 showing all significant effects. All effects of model 1 were significant except day length.

**Day Length Change Function**

Day length change at the day of feed intake affected sows feed intake during lactation in contrast to day length, which was not significant. Both functions were not exchangeable because day length did not become significant when day length change was omitted from the model. The regression coefficient for day length change was +0.18 (±0.028), meaning that sows consumed 0.36 kg more feed per day at the start of spring compared with the start of autumn.

**Temperature and Humidity**

The effects of both temperature and humidity on daily feed intake of sows during lactation were modeled, applying a quadratic function. For temperature, daily feed intake was greatest at 22.4°C, and sows ate

<table>
<thead>
<tr>
<th>Item</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parity</td>
<td>3.5</td>
<td>2.1</td>
<td>1</td>
<td>12</td>
</tr>
<tr>
<td>Lactation length, d</td>
<td>27.3</td>
<td>4.5</td>
<td>14</td>
<td>28</td>
</tr>
<tr>
<td>Number of piglets to be nursed</td>
<td>12.1</td>
<td>2.6</td>
<td>6</td>
<td>20</td>
</tr>
<tr>
<td>Daily feed intake, kg/d</td>
<td>5.31</td>
<td>2.17</td>
<td>0</td>
<td>9.0</td>
</tr>
<tr>
<td>Daily mean outside temperature, °C</td>
<td>12.8</td>
<td>3.5</td>
<td>−9.6</td>
<td>25.5</td>
</tr>
<tr>
<td>Maximum outside temperature, °C</td>
<td>14.2</td>
<td>7.3</td>
<td>−4.1</td>
<td>35.4</td>
</tr>
<tr>
<td>Daily mean relative atmospheric humidity, %</td>
<td>83.9</td>
<td>9.2</td>
<td>41</td>
<td>100</td>
</tr>
<tr>
<td>Daily mean room temperature, °C</td>
<td>25.2</td>
<td>1.4</td>
<td>17.9</td>
<td>30.3</td>
</tr>
<tr>
<td>Daily mean outside temperature, °C</td>
<td>11.4</td>
<td>6.3</td>
<td>−4.2</td>
<td>27.7</td>
</tr>
<tr>
<td>Maximum ambient room temperature, °C</td>
<td>26.1</td>
<td>1.8</td>
<td>18.4</td>
<td>36.0</td>
</tr>
<tr>
<td>Maximum outside temperature, °C</td>
<td>15.3</td>
<td>7.5</td>
<td>−2.6</td>
<td>34.5</td>
</tr>
</tbody>
</table>

1Weather station Eelde KNMI (Koninklijk Nederlands Meteorologisch Instituut).
2On farm measurement; only available on a subset of the data set (No. of sows = 363; No. of litters = 1,130; No. of days = 22,019).

**Figure 3.** Observed daily feed intake, its SD, and number of observations of primiparous (a) and multiparous sows (b) housed in a climate-controlled farrowing room for the maximum outside temperature, recorded daily over 24 h at the nearest weather station.
53 g/d less feed at the highest maximum 24-h outside temperature of 35.4°C [feed intake = 0.01385 ± 0.00300 (temperature) − 0.00031 ± 0.00009 (temperature²)]. For relative atmospheric humidity, daily feed intake was greatest at 80%. In comparison, daily feed intake was 145 g/d less at 40% relative atmospheric humidity and 37 and 35 g/d less at 60 and 100% relative atmospheric humidity, respectively [feed intake = 0.01443 ± 0.00620 (humidity) − 0.00009 ± 0.00004 (humidity²)]. Note, both thermal parameters were the temperature and humidity of the inlet air and thereby were not necessarily the temperature and humidity that sows experienced.

The F-value of both the linear and quadratic term of relative humidity per se was relatively low. From a biological point of view, this makes sense. Sows regulate their surface temperature by increasing or decreasing the blood flow subcutaneously. Therefore, sows lose the most heat through nonevaporative heat loss (radiation, convection, and conduction). Heat loss by respiration in pigs is low, although pigs are able to dissipate heat by respiration (Curtis, 1983).

Different interactions were tested to obtain a better understanding of effects. Among them, the interaction between temperature and humidity was evaluated. By including the interaction between maximum outside temperature and relative humidity in the model, the F-value of temperature and humidity was increased substantially. All 5 effects [humidity (linear and quadratic), maximum 24-h outside temperature at the nearest weather station (linear and quadratic), and humidity (linear) × maximum 24-h outside temperature at the nearest weather station (linear) interaction] became highly significant (P < 0.0001) with no change in the coefficient of determination. The decrease in daily feed intake with lower temperatures was more pronounced in combination with low humidity (Figure 4). For example, at a maximum 24-h outside temperature of −6°C, daily feed intake was 0.88 kg greater at 100% humidity in comparison with a humidity of 40%. In contrast, at a high outside temperature of 34°C daily feed intake actually increased with less humidity. However, this interaction was mainly observed for low humidity at low temperatures, which were represented by very few records given the mean and variation outlined in Table 1. In addition, the interaction did not improve the coefficient of determination, and humidity was neglected further on in our random regression models to prevent overparameterization of models.

**Line Crosses**

The interaction between temperature and line cross of the sow can be considered as the first step toward defining a reaction norm for a specific genotype. The

![Figure 4](image_url)

Figure 4. The effect of maximum 24-h outside temperature and relative atmospheric humidity measured at the nearest weather station on daily feed intake of sows during lactation housed in a climate-controlled farrowing room.
reaction norm of each sow line cross is shown for the 4 largest sow line crosses in Figure 5. These 4 largest sow line crosses consisted of 173, 145, 89, and 316 sows for cross A, B, C, and D, respectively, representing 85% of all sows available for this study.

Feed intake in lactating sows was greatest in the medium temperature ranges for 3 out of the 4 sow line crosses. Cross A and B responded similarly to temperature, although cross A had a greater feed intake. Cross D had a decreased feed intake capacity and could not handle extreme temperatures as well as cross A and cross B. The difference between maximum feed intake at 17°C and feed intake at 36°C was 0.22 kg/d for cross D. Cross C reacted differently. At temperatures below approximately 5°C, sows of this cross responded by eating more. Cross C can be considered as the least temperature sensitive line, which has been investigated further by Bloemhof et al. (2008).

**Random Regression**

Several tests were performed to evaluate the accuracy of random regression models. The mean feed intake curve derived from the fixed effects for primiparous and multiparous sows, applying model 3, were similar to those depicted in Figure 1 (panels a and b). The solutions for the fixed effects of line cross, day length change, number of piglets to be nursed, and parity of the sow were similar to those applying model 1 (results not shown). The fixed effect of maximum 24-h outside temperature was small. The difference in feed intake at −4.1°C compared with +35.4°C was less than 0.3 kg/d. This might be expected given the lack of variation in ADFI observed across the temperature trajectory (Figure 3, panels a and b). One of the reasons the results of model 3 differ slightly from those of model 1 is that we used a third-order Legendre polynomial for the fixed effect of temperature applying model 3, instead of a quadratic function applying model 1.

Average variance components over both trajectories, 28 d of lactation (model 2), and temperature (model 3) are presented in Table 3. Variances (additive genetic, permanent environment, and total), heritability, and repeatability per day of lactation are depicted in Figure 6 (panels a and b). A likelihood ratio test showed that every extra order of the polynomial, starting at the first order, contributed significantly to a better fit of the data \((P < 0.001)\). A fifth-order polynomial \((q = 5)\) for the random effects, applying model 2, did not reach convergence, and higher order polynomials were not tested.

The first 4 rows of Table 3 show that with increasing order of the polynomial, average heritability over the trajectory decreased. Average residual variance decreased, whereas average additive animal variance remained more or less constant. Average variance shifted toward permanent environment and batch effects. Additive variance over the trajectory increased with increasing day of lactation until a maximum was reached at about 3 wk in lactation (Figure 6, panel a). After 3 wk, additive variance decreased again. Total variance for each day in lactation \((\sigma^2_A + \sigma^2_{pe} + \sigma^2_h + \sigma^2_b)\) followed the shape of the feeding scheme except for the last 4 d of lactation, where the total variance increased rapidly. The latter effect was caused by an increased residual variance of the last error category (24 to 28 d). Heritability was highest during the first week of lactation and remained constant afterward (Figure 6, panel

![Figure 5](image-url) Reaction norms for sow line crosses of daily lactation feed intake records on maximum 24-h outside temperature measured at the nearest weather station.

![Figure 6](image-url)

### Table 3. Variance components, heritability \((h^2)\), and repeatability \((r^2)\) for daily feed intake during lactation, averaged over 28 d, applying random regression models, excluding the additive animal effect of temperature response (model 2) and including the additive animal effect of temperature response (model 3)\(^1\)

<table>
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<th>Model</th>
<th>(q)</th>
<th>(p)</th>
<th>(\sigma^2_{A0})</th>
<th>(\sigma^2_{pe})</th>
<th>(\sigma^2_h)</th>
<th>(\sigma^2_b)</th>
<th>(\sigma^2_{pe})</th>
<th>(\sigma^2_{p})</th>
<th>(h^2)</th>
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<td>0.1976</td>
<td>1.6569</td>
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<td>2</td>
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<td>0.21</td>
<td>0.69</td>
</tr>
</tbody>
</table>

\(^1q\) and \(p\) are orders of fit for the Legendre polynomials for the day effect and temperature effect, respectively; \(\sigma^2_A\) and \(\sigma^2_{pe}\) are the average additive variances for the day-dependent and temperature-dependent effect; \(\sigma^2_{pe}\) and \(\sigma^2_{p}\) are the average variances due to permanent environment for the day-dependent and temperature-dependent effect; \(\sigma^2_h\) is the average variance due to the batch effect; and \(\sigma^2_b\) is the average residual variance.
b). The decline in heritability from d 24 onward was caused by an increase in residual variance during the last 4 d of lactation. In comparison, repeatability was rather constant over lactation.

Adding an additive genetic effect of temperature response on feed intake (model 3) slightly reduced the average additive variance of feed intake over days (Table 3). With higher order of the polynomial, the additive and permanent environment variance of temperature response in feed intake increased. Goodness of fit improved up to the third-order polynomial ($p = 3$) for the temperature-dependent feed intake (likelihood ratio test: $P < 0.001$). The fourth order ($p = 4$) did not reach convergence. At the third-order polynomial, the additive variance of feed intake over temperature was less than 20% of the average additive variance of feed intake over days.

The average heritability was somewhat increased, excluding an animal and permanent environment effect of temperature response on feed intake. The day-dependent as well as the temperature-dependent permanent environmental effect on daily feed intake over days (Table 3). With higher order of the polynomial, the additive and permanent environment variance of temperature response in feed intake increased. Goodness of fit improved up to the third-order polynomial ($p = 3$) for the temperature-dependent feed intake (likelihood ratio test: $P < 0.001$). The fourth order ($p = 4$) did not reach convergence. At the third-order polynomial, the additive variance of feed intake over temperature was less than 20% of the average additive variance of feed intake over days.

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The overall genetic correlations at a fixed day in lactation (d 21) over the temperature trajectory are presented in the lower triangle of Figure 9, which shows that the overall genetic correlation between different temperature classes was high due to the high influence of additive genetic (co)variance of day. The upper triangle shows a steep decrease of the genetic correlation between temperature classes as the distance increases. The covariance between temperature classes remained positive within 1 SD ($\pm$) of the temperature class (Figure 9). For a larger distance, the covariance became negative, and the correlation between temperature classes decreased to approximately $-0.35$.

**DISCUSSION**

**Phenotypic Results**

Batch was used to account for differential effects such as management associated with the grouping. In addition, batch was at least partly confounded in this study.
Figure 8. Genetic correlations between daily feed intakes at different days in lactation. Below the diagonal: excludes temperature response (model 2); above the diagonal: includes temperature response (model 3).

Figure 9. Genetic correlations between daily feed intakes during lactation at different temperatures. Above the diagonal: temperature correlations exclusively. Below the diagonal: the overall genetic correlations at d 21 of lactation.
with temperature, humidity, and day length change. To prevent solving problems, batch was assigned a random effect, which has been shown to also benefit smaller contemporary group sizes (Van Vleck, 1987).

In the current study, sows were kept indoors in relatively small units where the ambient room climate was controlled by isolation, indirect air inlet, mechanical ventilation, and heating (when necessary). Nevertheless, the external climate had a considerable effect on feed intake of lactating sows. A maximum 24-h outside temperature, measured at the nearest weather station, only had a relationship with ambient room temperature when minimum indoor temperature was exceeded because no air cooling was applied and ventilation cannot, in the long run, prevent a rise in ambient room temperature. The correlation between outside humidity and ambient room humidity will be stronger compared with the correlation between outside and inside temperature because the exhaust fan reacted to temperature and not to humidity. Inlet air was heated at low temperatures, and consequently relative humidity dropped within the farrowing shed. At high outside temperatures, no heating or cooling of inlet air took place. The combined effects of these interactions might have contributed to the temperature × humidity interaction found in this study.

Ambient room temperature and ambient air quality within a room were partly related because in mechanically ventilated rooms, high ambient room temperature leads to high ventilation rates. To prevent energy losses, ventilation capacity was reduced at lower temperatures until it reached its minimum ventilation rate, which may have led to reduced air quality because air quality is expected to improve with greater ventilation rate. Increased ventilation rate also increases the airflow over the animals and assists with additional cooling. A repetition of our study in a less climate-controlled environment would show whether the effect of temperature on feed intake differs compared with conditions in which air quality and temperature might not be confounded.

High ambient temperature is known to reduce lactation feed intake (O’Grady et al., 1985; Koketsu et al., 1996; Gourdine et al., 2006). The real effects of high temperature on feed intake during lactation are probably more severe than found in this study. As soon as ambient room temperature was considerably above the desired ambient room temperature, general management precautions were implemented to prevent sows from stopping eating. The experimental farm implemented strategic processes, including no movement of sows during the hottest portion of the day, provision of extra water, and adjustment of feeding times to avoid the hottest portions of the day, in an effort to reduce the frequency of sows that stopped eating. Gourdine et al. (2006) compared ad libitum lactation feed intake of sows of 2 genetic lines during the warm and hot season in a tropical climate zone. The least temperature-sensitive line showed a small, almost equally sized, reduction in feed intake during nighttime. The most temperature-sensitive line showed a steep decrease in feed intake during nighttime and a minor decrease in feed intake during daytime. The latter indicates that management precautions to prevent sows from stopping eating, as performed on the experimental farm, might have limited the expression of sows to reduce their feed intake at higher temperatures and, therefore, might have contributed to reducing differences between sow genotypes.

As mentioned before, pigs regulate their body temperature mainly by increasing or decreasing subcutaneous blood flow. In case of heat stress, subcutaneous blood flow will increase and as a consequence blood flow will be decreased in the mammary gland (Black et al., 1993). It is expected that the effect of high temperatures on milk yield will be more severe than the effect on feed intake; therefore, higher temperature will have a greater influence on piglet development and growth due to less milk yield.

Phenotypic and genetic analyses in this study show that high as well as low (outside) temperatures affect feed intake during lactation. Most other studies focus on heat stress or heat tolerance [Quiniou and Noblet, 1999; S. Bloemhof (Institute for Pig Genetics, Beuningen, the Netherlands), A. Kause (Wageningen University, Wageningen, the Netherlands), E. Knol (Institute for Pig Genetics, Beuningen, the Netherlands), J. Van Arendonk (Wageningen University, Wageningen, the Netherlands), and I. Misztal (University of Georgia, Athens), unpublished data], probably because pig production is spreading to climates in which hot rather than cold thermoregulation is the critical issue.

### Random Regression

Heritability and repeatability estimates of average (restricted) feed intake over the entire lactation were 0.14 and 0.23, respectively, based on a data set, which overlapped to a large extent with the data used in the present study (Bergsma et al., 2008). In comparison, average heritability and repeatability during lactation were greater with estimates of 0.22 and 0.64, applying a random regression on day in lactation and ignoring a genetic temperature response. Further, batch was fitted as a random effect, which reduced ratios due to the larger phenotypic variance. A similar phenomenon was found by Lewis et al. (2010) who presented a heritability estimate of 0.17 based on random regression analysis of daily feed intake during lactation in comparison with a much greater repeatability of 0.74 due to the larger permanent environment effect of the sow. In beef cattle, the temporary environmental variance was predominantly partitioned into the animal permanent environment effect rather than the residual variance for BW over age using random regression models (Albuquerque and Meyer, 2001). In addition, a fifth- vs. a seventh-order model for additive genetic and animal permanent environment effects increased the permanent environment effect and decreased the additive ge-
The curve for animal variance followed the lactation maximum at d 20 was reached and decreased afterward. The number of observations for extreme temperature values was available. The extreme variances after d 24 contributed to greater permanent environment effect for milk yield in dairy cattle. 

Kolmodin et al. (2003) and van der Waaij (2004) suggested that selection for increased productivity in a nonlimiting environment resulted in an increased environmental sensitivity, which indicates a negative genetic correlation between the intercept and slope of the reaction norm model. Our study did not include the additive intercept for temperature. Therefore, the covariance between the additive intercept and slope of the temperature effect could not be estimated. Once we extended model 1 in PROC MIXED of SAS with a temperature (and temperature$^2$) × sow interaction, computer capacity was not large enough to estimate the effects for the entire data set. However, for the sow cross with the most number of observations only (sow cross D in Figure 5), the correlation between the level and the slope (linear and quadratic) was not significantly different from zero (results not shown). This correlation indicates that a greater feed intake of sows was not associated with greater sensitivity to temperature (environmental sensitivity).

For simplicity, the order of polynomials was chosen to be the same for all the random effects on day or on temperature-dependent feed intake. Pool et al. (2000) concluded that the additive genetic effects require a lower order of Legendre polynomials than the permanent environment effects for milk yield in dairy cattle.

Legendre polynomials generate a weight function with comparatively heavy emphasis on records at the outer parts of the interval for which they are defined compared with other functions (Meyer, 1998). A small number of observations for extreme temperature values was available. The extreme variances after d 24 of lactation and at high and low temperatures for the additive and permanent environment effect of temperature response on feed intake might originate from this phenomenon.

The additive variance for feed intake at different days of lactation increased from start of lactation until a maximum at d 20 was reached and decreased afterward. The curve for animal variance followed the lactation curve. Heritability, though, might be highest during the first week of lactation. Various studies have reported higher heritability estimates for more challenging environments (Pollott and Greeff, 2004; S. Bloemhof (Institute for Pig Genetics, Beuningen, the Netherlands), A. Kause (Wageningen University, Wageningen, the Netherlands), E. Knol (Institute for Pig Genetics, Beuningen, the Netherlands), J. Van Arendonk (Wageningen University, Wageningen, the Netherlands), and I. Misztal (University of Georgia, Athens), unpublished data). Apparently, this also holds for feed intake during lactation. For example, Bunter et al. (2010) found a higher heritability for lactation feed intake in medicated sows compared with unmedicated sows. Medication will predominantly be applied at the start of lactation after parturition, when sows are most vulnerable due to the stressors of parturition and the progress of sows from an anabolic state before farrowing to a catabolic state after parturition. In the present study, sows were fed a high-fiber diet during gestation and a high-energy diet during lactation. The digestive system of the sows had to adapt to the diet change. Changing diets is one of the risk factors for the occurrence of MMA (mastitis, metritis, agalactia) syndrome. The occurrence of this syndrome is heritable ($h^2 = 0.13$) as shown by Krieter and Presuhn (2009). Further, transition from colostrum to milk production takes place in the first week of lactation, adding to the physiological changes sows experience during the first week of lactation. Our finding of a higher heritability for daily feed intake during the first week of lactation was not observed by Lewis et al. (2010), who found minimal variation in heritability estimates for daily ad libitum feed intake (~0.03 to 0.06) during lactation.

Hermesch (2007) studied average lactation feed intake for d 1 to 5, d 6 to 10, d 11 to 15, and d 16 to 20 and reported heritabilities of 0.02, 0.17, 0.14, and 0.12 for these traits, respectively. Contrary to our findings applying random regression models, average feed intake during the first week of lactation was not heritable in the study by Hermesch (2007) given the nonsignificant heritability estimate of 0.02 ± 0.02. Applying a similar analysis to the data set used in the current study resulted in heritability estimates for the cumulative amount of feed eaten during the first, second, third, and fourth week of lactation of 0.05, 0.09, 0.18, and 0.12, respectively. Different conclusions based on either random regression analysis vs. examination of weekly cumulative (or average) feed intake traits seem to originate from different statistical properties of both approaches. For example, random regression analyses use data across the whole trajectory, which are ignored in univariate analyses of mean feed intake defined for specific periods of lactation.

In addition, making use of data from the whole lactation trajectory in random regression models might provide avenues to identify heritable environmental sensitivity in general. For example, the higher herita-
bility of feed intake during the first week (few days) of lactation may be the result of the more challenging circumstances during that period as discussed above, and one can hypothesize that this is caused by inheritable environmental sensitivity other than inheritable temperature sensitivity. This then raises the question whether it is possible to select for reduced specific environmental sensitivity.

**Alternative Approaches**

**Selection for Reduced Variation in Feed Intake.** Next to reaction norm models, there is a second approach to reduce environmental sensitivity, the conventional approach to explicitly define a fitness trait (Knap, 2005). Such a trait could be variation in day-to-day feed intake during lactation. If the effect of the sow n is expelled from model 1, the residual of every record (day) could be estimated applying model 1. The new fitness trait could be defined as the SD of the residuals per lactation. Animals who are less environmentally sensitive are expected to show a decreased SD. Highly sensitive animals are expected to demonstrate their sensitivity by a large difference in feed intake between days and thus show a greater SD. This approach ignores the underlying mechanism of variation of feed intake, but fits the definition of robust animals, which were defined as “pigs that combine high production potential with resilience to external stressors, allowing for unproblematic expression of high production potential in a wide variety of environmental conditions” (Knap, 2005). Feeding sows restrictively reduced the SD of feed intake per lactation artificially, which may explain the low heritability of the SD of the residuals per lactation found in this study of 0.07 (±0.03) and the low repeatability of 0.14 (±0.02). In addition, the SD in feed intake was genetically the same trait as the average feed intake, further reducing the usefulness of this trait as a selection criterion for reduced environmental sensitivity.

**Selection Against Heat Stress Applying a Linear Plateau Model.** Sows are exposed to heat stress when temperature exceeds the upper critical temperature (UCT) of the thermoneutral zone of the sow. The thermo-neutral zone is the zone between the lower critical temperature and the UCT of the animal in which no extra energy is expended to maintain body temperature. It could be hypothesized that reproductive performance of sows is unaffected within the thermoneutral zone and starts to decrease when temperature exceeds the UCT.

An approach to model environmental sensitivity that corresponds to the theory of Black et al. (1993) was proposed by Ravagnolo and Misztal (2000). Ravagnolo and Misztal (2000) extended a test day model for milk yield in dairy cattle with different rates of production decline with increasing temperatures. Their assumption was that the relative daily production of a cow is unaffected over a range of low and medium temperatures and then starts to decrease after a threshold, the UCT, assuming that genetic variability in susceptibility to heat stress exists. Bloemhof et al. (2008) and unpublished data from S. Bloemhof (Institute for Pig Genetics, Beuningen, the Netherlands), A. Kause (Wageningen University, Wageningen, the Netherlands), E. Knol (Institute for Pig Genetics, Beuningen, the Netherlands), J. Van Arendonk (Wageningen University, Wageningen, the Netherlands), and I. Misztal (University of Georgia, Athens) demonstrated that such a model is applicable in pigs for reproductive performance as well.

The implicit assumption underlying the model of Ravagnolo and Misztal (2000) is that the genetic correlation in temperature response at different temperatures above the UCT is high. As the results of the current study demonstrate, this might not always be the case. For that reason it is doubtful whether their model is applicable for lactation feed intake in sows. Taking an additive temperature response into account while estimating breeding values for feed intake during lactation reduces the error variance and thus improves accuracy of the breeding values. The approach of Ravagnolo and Misztal (2000) benefits from this phenomenon only beyond the UCT.

**Conclusions**

Day length changes, humidity, and temperature influence lactation feed intake in this order. Temperature effects were as large as 53 g/d between the greatest feed intake at 22.4°C and feed intake at 35.4°C. Humidity effects were as large as 145 g/d between the greatest feed intake at 80% humidity and feed intake at 40% humidity. In the present study, sows ate 360 g/d less at the start of autumn than at the start of spring.

Breeding for reduced thermal sensitivity of feed intake in lactating sows is possible, although the response will be small in a controlled environment of a farrowing facility located in a temperate climate zone. Appropriate higher order polynomial random regression models revealed a considerable permanent environmental effect for the influence of temperature on lactation feed intake. Genetic variance for lactation feed intake was approximately one-fourth of the permanent environmental variance. The animal that showed the largest decline in feed intake at 28.8°C (τ + 2σ) compared with feed intake at −0.4°C (τ − 2σ) ate 1.34 kg/d less at 28.8°C. This example demonstrates the magnitude of the combined effect of the permanent environment and the additive genetic temperature effect.

Statistical models become extremely complex. Random regression models are a useful tool to quantify the effect of temperature on feed intake during lactation, and results can be used to develop less complex models that can be implemented in practical breeding programs. Results may be specific to each environment, and therefore environments need to be described clearly.
LITERATURE CITED


