Anim. Res. 51 (2002) 227–243

DOI: 10.1051/animres:2002020

Original article

Effects of high ambient temperature and dietary protein level on feeding behavior of multiparous lactating sows

David RENAUDEAU[a]*, Nathalie QUINIOU[b], Serge DUBOIS[a], Jean NOBLET[a]**

[a] UMR sur le Veau et le Porc, Institut National de la Recherche Agronomique, 35590 Saint-Gilles, France
[b] Institut Technique du Porc, 35650 Le Rheu, France

(Received 6 September 2001; accepted 3 June 2002)

Abstract — Thirty-three multiparous Large White sows were used to determine the effect of high ambient temperature and level of dietary heat increment on their feeding behavior during lactation. Ambient temperature was maintained constant at 20 or 29 °C over 28-d lactation. The experimental diets fed during lactation were a control diet (NP; 17.6% crude protein) and two low protein diets obtained by the reduction of the CP level (LP, 14.6% CP) or both the reduction of CP and addition of 4% fat (LPF, 15.2% CP). The sows were given feed ad libitum between the 7th and the 27th day of lactation. Feeding behavior parameters were not influenced by diet composition. Between d 7 and d 27, daily feed intake decreased at 29 °C ($P < 0.001$; 4149 vs. 7444 $g \cdot d^{-1}$ at 20 °C); this was achieved by a concomitant reduction in meal frequency ($P < 0.001$; 6.5 vs. 9.4 $meals \cdot d^{-1}$) and in meal size ($P < 0.10$; 687 vs. 834 g per meal). The ingestion rate was not influenced by temperature (126 $g \cdot min^{-1}$ on average), and consequently the reduction of daily feed intake resulted in a decreased ingestion and consumption time (–25 and 28 $min \cdot d^{-1}$, respectively). The proportion of small meals (i.e., < 250 g) was higher whereas that of medium sized meals (i.e., 250–1000 g) was lower at 29 °C. Diurnal feed and water intakes represented 84% and 79% of total consumption, respectively. Two peaks in feed were observed, the first one between 07.00 and 13.00 at both temperatures and the second one that was shorter at 29 °C (17.00 to 23.00 vs. 14.00 to 23.00 at 20 °C). Standing activity averaged 127 $min \cdot d^{-1}$ with no significant difference between temperatures. About 70% of standing time was dedicated to feed and water consumption. As determined by the calculation of correlation coefficients between post- or pre-prandial interval and meal size, this latter seems to be partly regulated by satiety mechanisms in most sows (67%).

sows / high temperature / lactation / feeding behavior

---

* Present address: Unité de Recherches Zootechniques, INRA, Domaine Duclos, 97170 Petit Bourg, Guadeloupe, France.
** Correspondence and reprints
e-mail: noblet@st-gilles.rennes.inra.fr

Résumé — Effets des températures ambiantes élevées et du taux de protéines dans l'aliment sur le comportement alimentaire des truies multipares en lactation. Trente-trois truies multipares Large White × Landrace ont été utilisées pour déterminer l'effet d'une élévation de la température ambiante et du niveau d'extra chaleur alimentaire sur leur comportement alimentaire au cours de la lactation. La température ambiante est maintenue constante à 20 ou 29 °C au cours des 28 jours de lactation. Trois régimes expérimentaux ont été utilisés au cours de la lactation : un régime témoin (NP ; 17,6 % de matières azotées totales, MAT) et deux régimes à faible teneur en protéines (LP ; 14,6 % MAT) ou avec une réduction de la teneur en protéines et un ajout de matières grasses (LPF, 15,2 % MAT). L'aliment est distribué à volonté du 7^{e} au 27^{e} jour de lactation. Les paramètres du comportement alimentaire ne sont pas influencés par la composition des régimes. Entre le 7^{e} et le 27^{e} jour de lactation, la diminution de la consommation d'aliment à 29 °C (P < 0,001 ; 4149 vs. 7444 g·j^{-1} à 20 °C) est la conséquence d'une réduction de la réduction du nombre de repas (P < 0,001 ; 6,5 vs. 9,4 repas par jour) et de la taille des repas (P < 0,10 ; 687 vs. 834 g par repas). La vitesse d'ingestion n'est pas influencée par la température (126 g·min^{-1} en moyenne), et par conséquent, la réduction de la consommation d'aliment à 29 °C provoque une diminution du temps d'ingestion et de consommation (respectivement, –25 et –28 min·j^{-1}). A 29 °C, la proportion des repas de petite taille (i.e., < 250 g) est supérieure alors que celle des repas de taille moyenne (i.e., 250–500 g) est inférieure. La consommation d'aliment et d'eau en période diurne représente respectivement 84 et 79 % de la consommation totale. Deux pics de consommation sont observés, le premier entre 07.00 et 13.00 pour les deux températures et le second (17.00 à 23.00 à 29 °C vs. 14.00 à 23.00 à 20 °C) d'une durée plus courte à 29 °C. Le temps passé en position debout n'est pas affecté par la température et s'élève en moyenne à 127 min·j^{-1}. Environ 70 % du temps passé debout est dédié à la consommation d'aliment et d'eau. D'après les coefficients de corrélation calculés entre la taille du repas et l'intervalle de temps le séparant du repas précédent ou du repas suivant, il semble que pour la majorité des truies (67 %), la taille du repas soit partiellement régulée par des mécanismes de satiété.

truies / chaud / lactation / comportement alimentaire

1. INTRODUCTION

The adverse effects of high ambient temperatures on lactational performances have been well documented in sows. In practice, when ambient temperature increases above the thermoneutral zone (i.e., >18–20 °C), the voluntary feed intake decreases [3, 17, 24, 25], which reduces the heat production due to the thermic effect of feed. However, there is little information on the changes in feeding behavior associated with the reduction of voluntary feed intake in hot conditions. Recently, the effect of high ambient temperatures on the performance and feeding behavior in lactating sows were more accurately characterized [25–27]. The authors reported a non-linear reduction of feed intake with temperature increase with an accentuated reduction above 27 °C, associated first with a reduction of meal size and second with a reduction of both meal size and meal number at the higher temperatures.

According to the net energy system [22], starch and fat are more efficiently used than proteins. Consequently, diets with reduced crude protein content and (or) fat addition result in a lower heat production [16]. It can then be hypothesized that such diets would be better tolerated in hot conditions. Some results obtained in growing pigs or lactating sows support this hypothesis [33, 34].

The aim of the present study was to evaluate the effects of low-heat-increment diets on the performance and feeding behavior of lactating sows exposed to thermoneutral or hot temperatures. The results on lactation performance obtained on 59 sows have been previously published [30, 31]; they indicate that it is possible to attenuate the negative effect of hot temperature by using low heat increment diets. The present paper will focus on the feeding behavior aspects of the study with the results obtained on 33 of the 59 sows.

2. MATERIALS AND METHODS

2.1. Experimental design

A total of 59 multiparous Large White × Landrace sows, divided into eleven successive groups of four to six animals, were used in the experiment. Each group was kept in one of the two temperature controlled farrowing rooms used for the experiment and was exposed either at 20 °C or at 29 °C during a 28-d lactation period. The ambient temperature was maintained constant over the day. Within each group, feeding behavior could be characterized only on three sows using electronic troughs; a total of 33 sows were studied. After farrowing, sows were randomly allocated to three experimental diets: a diet with a standard crude protein (CP) level and low fat content (NP diet: 17.6% CP and 2.5% fat) and two diets with a reduced CP level not supplemented (LP diet: 14.2% CP and 2.6% fat) or supplemented with 4% vegetable fat (LPF diet: 15.5% CP and 6.1% fat). The three diets supplied the same level of digestible lysine (i.e., 0.82 g per MJ of net energy) and levels of digestible amino acids relative to lysine; vitamins, and minerals were similar in the three diets, and met or exceeded the NRC requirements [23]. Animal management and housing conditions were reported previously by Renaudeau et al. [31]. A simplified composition of the diets is presented in Table I; more details are given by Renaudeau et al. [30].

Experimental temperature was set up one day after farrowing. The photoperiod was fixed to 14 h of artificial light (08.30 to 22.30) and the minimum ventilation rate was 25 $m^3 \cdot h^{-1}$ per sow. The litter size was standardized to 12 piglets by cross fostering within the two days after birth. Heat was provided for piglets using infrared lamps and a heating mat. The infrared lamps were activated on the day of farrowing and switched off at d 3. After farrowing, in order to standardize feed intake until d 5, feed allowance was progressively increased by 1 $kg \cdot d^{-1}$; all sows were fed ad libitum from d 7. Sows had free access to water from a low-pressure nipple located out of the feeder and connected to a 55-L graduated water bank. Creep feed was offered to piglets from 21 d post-partum. The day before weaning (i.e., d 27), refusals were collected at 16.00 in order to weigh sows with an empty digestive tract the following morning.

2.2. Measurements

Body weight (BW) and backfat thickness were measured after farrowing and at weaning. Backfat thickness was measured ultrasonically 65 mm from the middle line at the last rib (P_2 site). Piglets were individually weighed at birth and at weaning. Every morning, refusals were manually collected between 08.30 and 09.00 and fresh feed was offered thereafter. For the total lactation period, average daily feed and water intakes were determined as the difference between feed allowance and the refusals collected on the next morning. The weaning to estrus interval was determined visually using an aerosol reproducing the odor of the boar (Boarmate®, ANTEC, France).

During the ad libitum period (i.e., from d 7 to d 27), individual feeding and drinking behavior were recorded using a trough and a tank both connected to a computer through load cells as previously described by Quiniou et al. [27]. Briefly, after each visit (i.e., feeding or drinking bouts), time at the beginning and at the end of the visit and feed or water consumption were recorded. Standing duration (min) was continuously measured by using an infra red barrier located in the middle of the crate.

Table I. Composition of the experimental diets.

Diet[a]	NP	LP	LPF
Ingredients, g·kg^{-1}			
Wheat	350	403	364
Corn	353	406	366
Soybean meal	207	91	129
Wheat bran	30	30	30
Sugar beet molasses	20	20	20
Soya oil			40
L-lysine HCL	1.7	5.5	5.3
DL-methionine	0.4	1.5	1.7
L-threonine	0.9	2.5	2.7
L-tryptophan		0.6	0.6
L-isoleucine		1.3	1.4
L-valine		2.2	2.3
Dicalcium phosphate	16	16	16
Calcium carbonate	11	11	11
Salt	5	5	5
Vitamins and trace minerals mixture	5	5	5
Chemical composition, g·kg^{-1} (as fed)			
DM	873	874	881
Ash	51	50	55
Crude protein	176	142	152
Crude fat	25	26	61
Starch	432	495	447
Crude fiber	22	20	19
Lysine	9.6	9.5	10.4
Methionine + cystine	6.0	6.0	6.4
Threonine	6.9	6.7	7.4
Energy value, MJ·kg^{-1} [bc]			
Digestible energy	14.7	14.4	15.2
Metabolisable energy	14.2	14.0	14.8
Net energy	10.5	10.6	11.2

[a] NP for normal protein, LP for low protein and LPF for low protein and added fat. [b] Values measured on non-pregnant adult sows (4 measurement per diet). [c] Adjusted for measured DM on the pooled samples. ME was estimated from DE content and the ME/DE ratio was assumed to be equal to those measured in growing pigs fed the same diets (96.2, 97.2 and 97.2% for NP, LP and LPF diets, respectively; [15]). NE was estimated from measured digestible energy content (MJ·kg^{-1} DM) and the chemical component (g·kg^{-1} DM) according to Noblet et al. [22].

2.3. Calculations and statistical analysis

A meal can be split into successive bouts separated by a short within-meal pause detection which depends closely on the system used for the determination of the feeding behavior parameters. To allow comparison with the results from other studies obtained with different systems, successive visits belonging to the same meal need to be grouped into the same meal. For this purpose, the "meal criterion" is defined as the maximum length of the within-meal interval between visits [2, 9, 13, 15]. In other words, when two successive visits are separated by an interval longer than the meal criterion, they are not considered as belonging to the same meal.

Table II. Effects of ambient temperature and diet composition on the performance of lactating sows and their litter (adjusted means).

Items	Temperature, °C	20			29				
	Diet [a]	NP	LP	LPF	NP	LP	LPF	RSD [b]	Statistical analysis [c]
No. of sows		5	5	5	6	6	6		
Parity		2.4	2.8	2.8	2.8	2.8	3.2	0.8	
Duration of lactation, d		28.0	28.6	29.4	28.3	27.8	27.8	0.8	T*
Feed intake, $g \cdot d^{-1}$									
From farrowing to weaning		6332	6364	6971	3297	3752	4047	857	T***
From d 7 to d 27		7189	7435	7551	3596	4160	4468	1013	T***
Net energy intake from d 7 to d 27, $MJ \cdot d^{-1}$		74.7	78.6	85.0	37.4	44.0	50.3	10.9	T***, D†
Body weight, kg									
After farrowing		257	256	263	267	263	255	15	G***
Loss during lactation		19	16	14	46	33	30	14	T***
Backfat thickness, mm									
After farrowing		22.4	22.3	19.7	18.3	22.8	20.4	2.9	D†, T × D†, G†
Loss during lactation		4.4	3.8	1.6	4.4	4.8	3.3	2.6	
Weaning to estrus interval, d [d]		4.8	4.8	4.9	4.0	5.2	4.5	1.1	G†
Mean litter size during lactation		10.6	10.7	10.4	10.2	11.1	10.4	0.9	G**
Litter growth rate, $kg \cdot d^{-1}$		2.74	2.83	22.80	2.13	2.33	2.25	0.53	T**
Weaning body weight, kg per piglet		8.79	9.25	9.60	7.71	6.71	7.94	1.10	T**

[a] NP = normal protein diet, LP = low protein diet, and LPF = low protein diet and added fat.
[b] Residual standard deviation.
[c] From an analysis of variance including the effects of ambient temperature (T), diet composition (D), interaction between temperature and diet composition (T × D), and the effect of the group of sows within temperature (G). Statistical significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.
[d] Mean calculated from 31 values; one sow was slaughtered after weaning and one did not display estrus within the 14 days following weaning.

The meal criterion was estimated using the log survivor curve technique as described by Bigelow and Houpt [2]. A sample of 280 daily values were calculated from 27 sows exposed to both temperatures studied. The mean value of the meal criterion was then 1.10 (± 0.73) min. Ninety-six percent of the individual meal criteria were below or equal to 2 min; this value was chosen for further calculation of daily components of feeding behavior criteria. These components were the total daily number of visits and meals, the total feed (g) and water intake (L), the total ingestion time per day (the sum of the duration of the visits, min), total consumption time per day (sum of ingestion time and within-meal intervals, min), average rate of feed intake (total feed intake/total ingestion time, g/min), and average ingestion time per meal (total ingestion time/total number of meals, min).

The effects of ambient temperature, diet composition, their interactions on the mean lactation performances (d 0 to d 28) were tested through an analysis of variance (General Linear Model procedure of SAS [32]). The effect of the group of sows was tested within the effect of ambient temperature. Over the ad libitum feeding period (d 7 to d 27), 699 daily measurements of the components of feeding behavior were performed from the 33 sows. These values were averaged per sow on a daily basis over the whole period (d 7–d 27) or over three sub periods (P1, P2 and P3) corresponding to d 7 to d 13, d 14 to d 20 and d 21 to d 27, respectively. The former components of feeding and drinking behavior (d 7 to d 27) were submitted to an analysis of variance including the same effects as described above; the latter ones were analyzed according to a multifactorial design (split plot, General Linear Procedure of SAS, [32]) including the effects of period, temperature, diet composition, light, animals, and their interactions. In addition, the mean components per sow over the whole period were calculated according to the light regimen that were also analyzed according to the same multifactorial design including the effects of the photoperiod (light vs. dark period) instead of the period.

Continuous recording of feed and water consumption, ingestion time (feed and water), and duration of standing were pooled per hour. These data were analyzed through a repeated measurement analysis of variance (General Linear Model SAS [32]) according to the comparison of hourly values to a reference value and from the generation of contrasts between the adjacent hourly values.

In addition, for each sow, individual meals performed between d 7 and d 27 were divided into nine classes according to their size. The effects of temperature on meal partition among classes were tested through an analysis of variance (General Linear Model SAS [32]) with temperature, diet, meal size class as main factors and interactions. In order to study what determines meal size, correlation coefficients between meal size and the meal duration, the size of the following meal, and the pre-prandial (i.e., time interval elapsed since the previous meal) and post-prandial intervals (i.e., time interval elapsed before the following meal) were calculated. Such calculations were performed from all meals obtained from all sows and also for each sow. Since these data were not normally distributed, they were submitted to a logarithmic transformation before calculation of the Pearson correlation coefficients [32]. The effect of temperature on the correlation coefficients was analyzed according to the method of standard error with a previous inverse tangent transformation (or z-transformation [6]).

3. RESULTS

The sow parity number averaged 2.8 (Tab. II). One group of sows exposed at 29 °C had a shorter lactation length which resulted in a subsequent shorter average

Table III. Effect of ambient temperature and diet composition on feeding behavior, water intake and duration of standing of lactating sows (d 7 to d 27; adjusted means).

Items / Temperature, °C	20			29				
Diet [a]	NP	LP	LPF	NP	LP	LPF	RSD [b]	Statistical analysis [c]
No. of meals	11.1	8.2	8.9	6.8	6.1	6.6	1.9	T***
Feed intake								
$g \cdot d^{-1}$	7452	7474	7408	3936	4104	4407	943	T***
g per meal	710	928	864	643	730	688	218	$T^{\dagger}$
Net energy intake, $MJ \cdot d^{-1}$	77.5	79.0	83.4	40.9	43.4	49.6	10.2	T***
Feed ingestion time								
$min \cdot d^{-1}$	60.2	58.3	57.8	33.9	32.1	36.8	8.1	T***, $G^{\dagger}$
min per meal	5.9	7.3	6.6	5.3	5.6	5.6	1.6	$T^{\dagger}$
Feed consumption time, $min \cdot d^{-1}$	62.8	65.8	61.4	36.8	37.2	39.0	8.2	T***, $G^{\dagger}$
Rate of feed intake, $g \cdot min^{-1}$	127	132	129	119	129	123	15	G**
Water intake [d]								
$L \cdot d^{-1}$	24.1	26.4	36.7	23.0	27.4	34.3	8.6	D*, G*
$L \cdot kg^{-1}$ of feed	3.2	3.5	4.8	6.2	6.7	7.9	2.1	T***
Water ingestion time, $min \cdot d^{-1}$ [d]	30.1	37.5	33.9	44.0	48.3	41.3	20.6	$D^{\dagger}$
Standing activity, $min \cdot d^{-1}$ [d]	123	141	150	121	100	124	41	

[a] NP = normal protein diet, LP = low protein diet, and LPF = low protein and added fat diet.
[b] Residual standard deviation.
[c] From an analysis of variance including the effects of ambient temperature (T), diet composition (D), interaction between temperature and diet composition (T × D), and the effect of the group of sows within temperature (G). Statistical significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.
[d] Water consumption and standing duration values correspond to the mean of available values because of water spillage and infrared barrier malfunction, some values were calculated on less than 21 days.

Table IV. Effect of ambient temperature and photoperiod on feeding behavior of lactating sows (d 7 to d 27; adjusted means).

Temperature, °C	20		29			
Items	Day	Night	Day	Night	RSD [a]	Statistical analysis [b]
No. of sows	15	15	18	18		
No. of meals	7.6	1.9	5.4	1.1	1.1	T***, L***, T × L*
Feed intake						
$g \cdot d^{-1}$	6160	1300	3536	614	698	T***, L***, T × L***
g per meal	848	757	701	629	211	T†, A**
% of total feed intake	82.7	17.3	85.2	14.8	6.3	
Ingestion time						
$min \cdot d^{-1}$	47.8	11.0	28.4	5.9	5.7	T***, L***, T × L***
min per meal	6.6	6.5	5.4	5.6	1.9	
Consumption time, $min \cdot d^{-1}$	53.2	12.6	31.3	6.3	6.1	T***, L***, T × L***
Rate of feed intake, $g \cdot min^{-1}$	131	122	127	114	20	L*
Water intake, $L \cdot d^{-1}$ [d]	22.7	6.4	23.7	4.5	5.5	D*, L***
Standing activity, $min \cdot d^{-1}$ [d]	114	24	94	21	24	L***

[a] Residual standard deviation.
[b] From a split-plot analysis of variance including the effects of ambient temperature (T), diet composition (D), light (L), animal (A), and interactions. Statistical significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.
[d] Water consumption and standing duration values correspond to the mean of available values because of water spillage and infrared barrier malfunction, some values were calculated on less than 21 days.

duration of lactation at 29 °C (28.0 vs. 28.7 d at 20 °C, $P < 0.05$). Exposure to hot climatic conditions (29 vs. 20 °C) resulted in a lowered voluntary daily feed intake, a higher BW loss and lighter piglets at weaning. The performances were not affected by diet composition (Tab. II). None of the feeding behavior criteria was influenced by diet composition (Tab. III). However, the daily number of meals was numerically lower for the low protein diets (7.5 for LP and LPF diets vs. 9.0 meals per day for the NP diet, $P = 0.10$). Compared to 20 °C, exposure to 29 °C induced a decrease of the daily number of meals (6.5 vs. 9.4 meals per day, $P < 0.001$) and tended to reduce their size (687 vs. 834 g per meal, $P = 0.07$). Consequently, daily feed intake decreased significantly from 7444 to 4149 g·d^{-1} when the sows were kept at 29 °C. The ingestion rate was not affected by temperature ($P > 0.10$) and averaged 126 g·min^{-1}. Subsequently, feed intake and daily ingestion and consumption times were reduced at 29 °C (–24.5 and –28.0 min·d^{-1}, respectively when compared to 20 °C, $P < 0.001$).

Because of excessive water spillage and infrared barrier malfunctions, 23 and 59 observations were missing for these two criteria out of a total of 699 expected. From available data, it appears that ambient temperature did not affect daily water intake between d 7 and d 27 which resulted in a higher water:feed ratio at 29 °C (6.9 vs. 3.8 L·kg^{-1} at 20 °C, $P < 0.001$). The total ingestion activity was calculated as the sum of ingestion times of feed and water. Temperature had no effect on standing activity or total ingestion activity ($P = 0.12$); however those values were numerically lower at 29 °C than at 20 °C (115 vs. 138 min·d^{-1} and 79 vs. 93 min·d^{-1}, respectively; Tab. III).

As presented in Table IV, feeding behavior was mainly diurnal. Meal size was similar during the night and the day. The rate of feed intake was reduced during the nocturnal period (118 vs. 129 g·min^{-1}, $P = 0.05$). Diurnal water intake represented about 79% of total water intake which is close to the value obtained for feed intake; in addition its partition between day and night was not affected by temperature.

As illustrated in Figure 1, the kinetics of feed intake over the 24 h-period showed a bimodal partition of feed consumption as obtained from the comparison of hourly feed intake to the average value recorded between 00.00 and 02.00 (considered as the

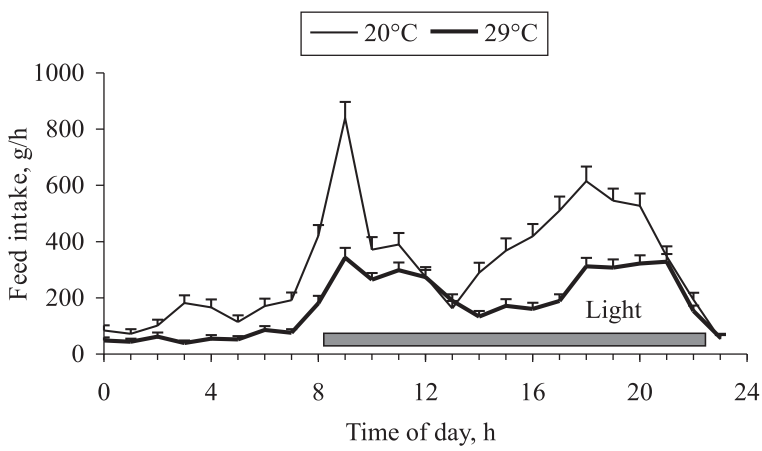

Figure 1. Effect of ambient temperature and time on the kinetics of daily feed intake in lactating sows (mean + standard error); each point is the mean of 15 sows at 20 °C and 18 sows at 29 °C.

reference value) or the hour to hour variation of feed intake. The first peak was observed between 07.00 and 13.00 at both temperatures. The second peak took place later during the light-period and was shorter at 29 °C (i.e., 17.00 to 23.00) than at 20 °C (i.e., 14.00 to 23.00). Exposure to 29 °C significantly reduced ($P < 0.05$) mean feed intake between 03.00 and 11.00 and between 15.00 and 20.00. Irrespective of the temperature, sows consumed about 37 and 57% of their total feed intake during the first and the second feeding peaks, respectively.

The pattern of hourly water intake was quite similar to that observed for feed with two peaks at both temperatures (between 07.00 and 13.00 and between 14.00 and 22.00; with basal values between 23.00 and 00.00) (Fig. 2). As described in Figure 3, standing activity was highly correlated (r = 0.85) with total ingestion time; standing activity exceeded ($P < 0.05$) feeding and drinking time, except between 00.00 and 05.00.

Daily feed intake increased ($P < 0.05$) from period 1 to period 3 at both temperatures (Tab. V). The duration of period 3 was lower at 29 °C in connection with the shorter duration of the overall lactation period at this temperature. No interaction was observed between the period of lactation and ambient temperature for any component of the feeding behavior. Ingestion and consumption times tended to be higher in period 3 compared to period 1 at both temperatures. The number of meals remained constant ($P > 0.10$) over the three periods. The variation of meal size was not significantly different between the periods. The daily water consumption was higher during period 3 than during periods 1 and 2 (33.7 vs. 26.0 $L \cdot d^{-1}$ on average).

The Pearson correlations between meal size and the pre- and post-prandial intervals, duration of meal and meal size of the following meal are listed in Table VI. Strong relationships were obtained between meal size and duration (r = 0.87–0.88) in relation with the constancy of the rate of feed intake. Correlation coefficients between meal size and other components of feeding behavior were low (r = 0.10–0.37) but significant. The correlation coefficients were not markedly affected when variations of meal criterion were performed. Ambient temperature

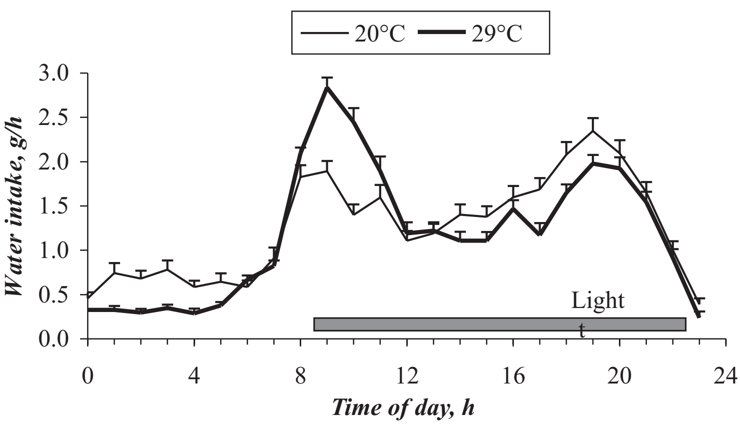

Figure 2. Effect of ambient temperature and time on the kinetics of water consumption (mean + standard error); each point is the mean of 15 sows at 20 °C and 18 sows at 29 °C.

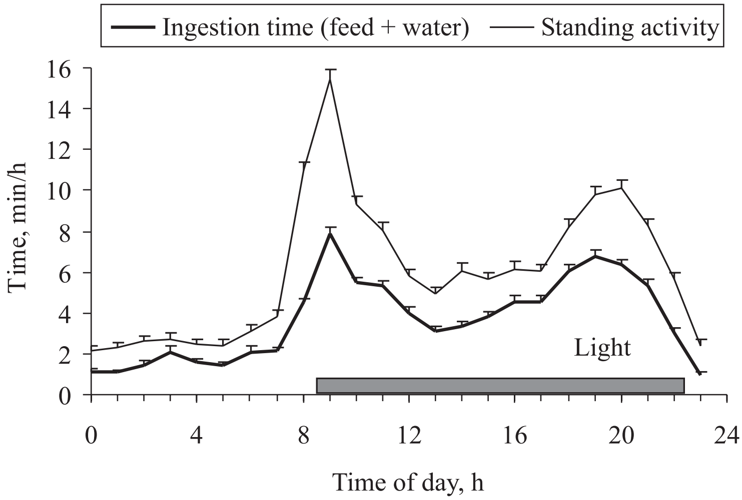

Figure 3. Effects of time on the kinetics of ingestion time (feed + water) and standing activity time (mean + standard error); each point represents the mean of all 20 °C and 29 °C sows (n = 33) over 21 days.

did not affect most of the correlation coefficients; however, they were numerically higher at 20 °C.

4. DISCUSSION

The 33 sows used in the experiment are a part of a larger group of 59 sows for which lactation performances were presented in previous papers [30, 31]. On average, their daily feed intake was slightly lower than for the 59 sows at both temperatures (– 250 and – 150 $g \cdot d^{-1}$ at 20 and 29 °C, respectively) whereas BW and backfat losses, and litter growth rate were not significantly different. In addition, daily feed intake increased after d 6 at both temperatures which is in agreement with the increase of feed intake observed between periods 1 and 3 for the 33 sows. Overall, the sows used to measure feeding and drinking behavior can be considered as representative of all sows used in the trial.

At 20 °C, 83 and 76% of feed and water intake, respectively, occurred during the 14-h light period. With a similar photoperiod, Quiniou et al. [26] reported that 82% of feed intake occurred during the daytime on average at 18 and 22 °C. These values were slightly lower than the 90% obtained by Weldon et al. [35] in primiparous sows kept at 21.5 °C but with a 16 h light: 8 h dark regimen. Moreover, the diurnal repartition between day and night depends on ambient temperature, either when it is kept constant [26] or when it fluctuates [27].

Feeding and drinking activity were mainly diurnal with two peaks feeding or drinking activity: a smaller peak in the morning compared to a larger peak in the beginning of the afternoon. The first peak corresponds to the time when the staff of the experimental farm started to work and when feed distribution occurred. The second peak was not related to such events. This bimodal feeding activity during lactation could be partly related to the feeding pattern in pregnancy. Dourmad [11] suggested that the bimodal feeding pattern could be explained by diurnal hormonal variations implicated in the metabolic

Table V. Effect of ambient temperature and period of lactation on feeding behavior of lactating sows (d 7 to d 27; adjusted means).

Items	Temperature, °C	20			29				
	Period [a]	1	2	3	1	2	3	RSD [b]	Statistical analysis [c]
No. of meals		9.7	10.3	8.9	6.2	6.9	6.7	2.7	T*, A**
Feed intake									
$g \cdot d^{-1}$		7033	7394	7516	3898	4234	4469	820	T*, P*, A***
g per meal		819	767	880	694	674	715	209	A***
Ingestion time									
$min \cdot d^{-1}$		57.4	59.1	61.0	28.7	37.1	38.0	11.7	T*, P†
min per meal		6.5	6.2	7.2	5.0	5.6	5.9	1.8	
Consumption time, $min \cdot d^{-1}$		63.7	66.4	67.9	30.9	40.8	42.1	12.2	P†
Rate of feed intake, $g \cdot min^{-1}$		128	128	125	136	122	122	27	A†
Water intake [d]									
$L \cdot d^{-1}$		25.5	26.2	32.0	25.6	26.7	35.3	1.9	P**, A***
$L \cdot kg^{-1}$ of feed		3.6	3.5	4.2	6.6	6.6	8.1	1.9	P*, A***
Standing activity, $min \cdot d^{-1}$ [d]		137	125	149	111	121	126	44	A*

[a] Periods 1, 2 and 3 correspond to days 7 to 14, days 15 to 21, and day 22 to the day before weaning, respectively; duration of week 3 was, 7.7 and 7.0 days at 20 and 29 °C, respectively.
[b] Residual standard deviation.
[c] From a split-plot analysis of variance including the effects of ambient temperature (T), diet composition (D), period (P), animals (A) and interactions. Statistical significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.
[d] Water consumption and time in standing position values correspond to the mean of available values of the ad libitum period (from d 7 to d 27); because of a water spillage and an infrared barrier malfunction, less than 21 values were available for some sows.

Table VI. Pearson correlation coefficients between meal size and different components of feeding behavior as a function of the meal criterion.

Variables	Temperature	Meal criterion, min				
		1	2	5	10	a
Total number of meals						
	20	3313	2796	2508	2340	
	29	2681	2400	2260	2776	
Meal size / meal duration						
	20	0.88[d]	0.89[d]	0.89[d]	0.90[d]	***
	29	0.86[d]	0.85[d]	0.84[d]	0.83[d]	***
Meal size / pre-meal interval[b]						
	20	0.29[d]	0.39[d]	0.39[d]	0.37[d]	***
	29	0.38[e]	0.35[d]	0.34[d]	0.27[d]	***
Meal size / post-meal interval[c]						
	20	0.19[d]	0.28[d]	0.39[d]	0.39[d]	***
	29	0.25[d]	0.29[d]	0.34[d]	0.34[d]	***
Meal size / following meal size						
	20	0.23[d]	0.26[d]	0.29[d]	0.27[d]	***
	29	0.23[d]	0.19[d]	0.18[e]	0.14[e]	***

[a] ** Pearson correlation coefficients significantly different from zero ($P < 0.01$).
[b] Time interval elapsed since the previous meal.
[c] Time interval elapsed before the following meal.
[d, e] Effect of temperature. Within a column, Pearson correlation coefficients not followed by the same superscript differ ($P < 0.01$).

utilization of nutrients or in gastric emptying. Moreover, the two intensive periods of feeding occurred near the time lights are switched on or off and consequently, feeding activity could also be driven by light change in the farrowing room.

According to our results, daily ingestion time was reduced under hot exposure in connection with a decrease of feed intake. The standing activity was highly correlated to total ingestion time; on average, about 70% of standing time was dedicated to feed and water consumption. Total ingestion time and consequently standing activity were reduced between 20 and 29 °C. According to the high energy cost of standing in sows [21], this suggests that the reduction in standing activity at 29 °C contributes, in addition to feeding behavior adaptation, to a reduction in heat production in hot conditions.

In our study, the adopted value for the meal criterion was 2 min; this agreed with the value calculated by Quiniou et al. [26] in lactating sows, Collin et al. [5] in weaned pigs, and Labroue et al. [15] and Quiniou et al. [28] in growing pigs using a comparable feeding station (a trough placed on load cells). With infrared barriers used to detect feeding bouts, Dourmad [11] reported a longer meal criterion (i.e., 10 min). In fact with this latter system, the infrared beam was cut as soon as the sow lowered its head to the trough which occurs even during the

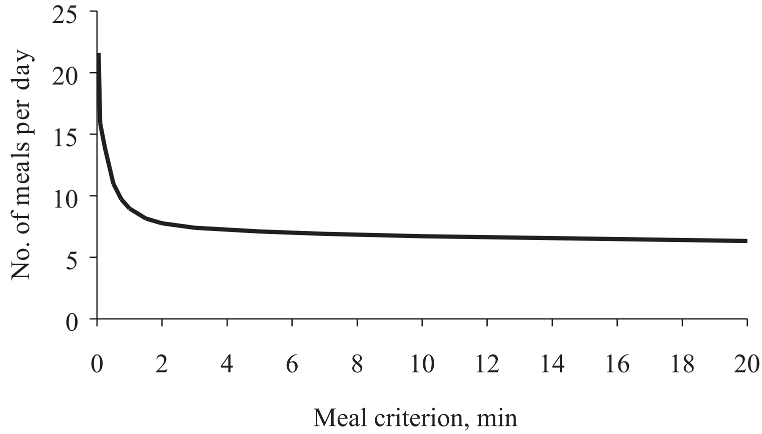

Figure 4. Effect of meal criterion variations on the calculation of the daily meal frequency (No. of calculations = 699 days).

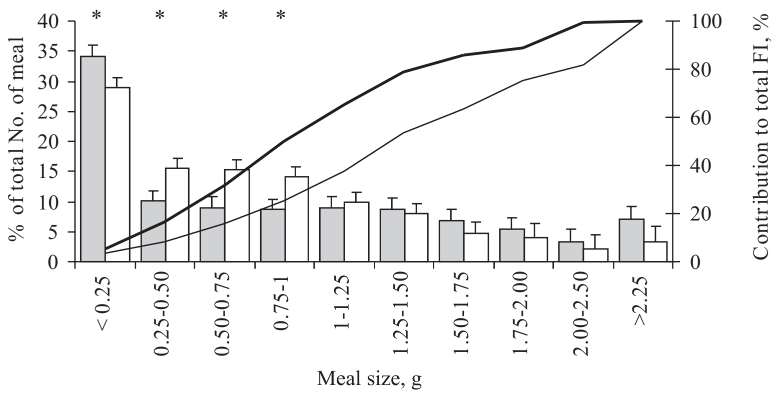

Figure 5. Effect of ambient temperature on distribution of meals (grey bars: 20 °C; white bars: 29 °C) and contributions to daily feed intake (normal line, 20 °C and bold line, 29 °C) according to meal size class. * proportion of meals differs ($P < 0.01$) between temperatures.

within meal pauses. In their studies, Weldon et al. [35] and Ermer et al. [12] visually checked the time spent to eat and weighed the amount of feed consumed after each meal at given stages of lactation; they considered 10 and 20 min, respectively, as corresponding to the meal criterion. This latter methodology would not be quite appropriate to discriminate feeding and non feeding intervals in contrast with our system which only detects feeding bouts. As illustrated in Figure 4, an underestimation of the meal criterion results in an important increase of the number of meals, while an overestimation has little effect. This also indicates that the components of feeding behavior calculated in the present study can be compared with those calculated by Dourmad [11], Weldon et al. [35], and Ermer et al. [12], except for consumption time because of the longer meal criterion used in the latter studies.

Over the ad libitum period, the daily meal frequency averaged 9.4 at 20 °C which was higher than the value reported in multiparous sows by Quiniou et al. [26] (7.1 meals per day on average at 18 and 22 °C) and Ermer et al. [12] (7.0 meals per day on d 21 at 24 °C). Nevertheless, closer values were reported in primiparous sows by Dourmad [11] (9.0 meals per day under uncontrolled temperature ranging between 18 and 25 °C) and Weldon et al. [35] (8.0 meals per day at 21.5 °C). In our study, meal size (834 g) was close to the value reported by Weldon et al. [35] (750 g) and intermediate between the values reported by Quiniou et al. [26] and Ermer et al. [12] (1172 and 1200 g per meal, respectively) and with the lowest ones reported by Dourmad [11] (544 g per meal).

In order to evaluate the meal size distribution and the contribution of individual meals to total daily feed consumption, the meals were classified according to their size. As illustrated in Figure 5, a great proportion of meals have a minor contribution to total feed intake; the small meals (< 250 g) represented 32% of the total number of meals but contributed to only 4.5% of feed intake and they could have a relatively large influence on feeding parameter determination. However, the proportion of small meals was quite variable between sows (i.e., 5 to 58% of total meals). This suggests a large individual difference in meal patterns between animals that belong to different sub-populations: the nibbler sows and the greedy ones. In addition, it could be estimated that about 40% of the meals represented about 90% of the feed intake. In agreement with Dourmad [11], these results emphasize the difficulty to define what is a meal in lactating sows.

As observed for the 59 sows, an increase in ambient temperature between 20 and 29 °C depressed daily feed intake during the whole lactation period and over the ad libitum feeding period (– 2857 and – 3316 $g \cdot d^{-1}$, respectively). The decrease of voluntary feed intake at 29 °C was mainly related to a reduced number of meals as previously showed by Quiniou et al. [26] and to some extent to a reduced meal size. In addition, the proportion of small meals (i.e., < 250 g) was higher whereas that of medium sized meals (i.e., 250 < meal size < 1000 g) was lower at 29 °C (Fig. 5). According to the results obtained by Nienaber et al. [19], Quiniou et al. [28] and Collin et al. [5] in group housed weaned pigs and growing pigs kept at temperatures similar to those of the present study, the effect of high temperature on voluntary feed intake was achieved by a reduction of meal size while the number of meals remained relatively constant. This was in agreement with Quiniou et al. [26], suggesting that for a given level of high temperature (e.g., 29 °C), heat stress is more severe for sows than for weaned or growing pigs. These authors hypothesized that the elevation of ambient temperature firstly affects meal size and secondly, both the number and size of the meals. The decrease of meal frequency in hot conditions is in agreement with the thermostatic theory of feed intake control. According to this theory, the initiation of meal occurs when the inhibitory effect of high body temperature due to feeding is reduced [10]. The strong increase of body temperature observed at 29 °C [30] would result in a diminished signal initiating feed intake and concomitantly in a decrease in meal frequency. According to the decreased meal size obtained in hot conditions or when sows are fed with low-heat-increment diets, the reduction of meal size could also be interpreted as an adaptation to reduce heat production.

No significant effect of high ambient temperature on rate of feed intake was observed in lactating sows in the present study which is in agreement with the results obtained for sows, and weaned and growing pigs [5, 20, 26, 28]. In a recent literature review, Quiniou et al. [29] reported a positive relationship between the rate of feed intake and BW. This would indicate that the rate of feed intake was related to the maturity of the sows (i.e., mouth and gut size) and little dependent on the ambient temperature.

Correlation coefficients between meal size and pre- and post-meal intervals, meal duration, and the size of the following meal were not improved when longer meal criterion were used; this contrasted with the results of de Castro [7] and Castonguay et al. [4] in rats. For this reason, a 2-min meal criterion was chosen to compare the correlation coefficients. The relationship between meal size and pre-prandial interval was slightly higher than with the post-prandial one (0.37 vs. 0.28) being in agreement with the results of Labroue [14] in growing pigs. Correlations between meal size and pre-meal interval were calculated for each sow: pre- and post-prandial correlations were different from zero ($P < 0.01$) for 67% and 45% of the sows, respectively. These results supported the hypothesis according to which feed intake can be regulated by a satiety mechanism rather than by a hunger mechanism for most of the sows [36]. Montgomery et al. [18] did not report a significant correlation between meal size and pre- and post-meal intervals in growing pigs. A significant positive correlation between meal size and post-meal interval was reported by Auffray and Marcilloux [1] in 50% of their pigs and by de Castro [8] in rats. Overall, these results indicate that the regulation of the initiation of feed intake remains unclear. Factors other than satiety or hunger mechanisms (an individual circadian rhythm of sows, environmental factors, facilitation between sows, etc.) could be implicated.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge Degussa (Hanau, Germany) and Ajinomoto Eurolysine (Paris, France) for their financial support, Institut Technique du Porc (France) for the grant of D. R., and P. Bodinier, S. Daniel, J. Gauthier, and H. Renoult for their technical assistance.

REFERENCES

[1] Auffray P., Marcilloux J.C., Analyse de la séquence alimentaire du porc, du sevrage à l'état adulte, Reprod. Nutr. Dev. 20 (1980) 1625–1632.

[2] Bigelow J.A., Houpt T.R., Feeding and drinking patterns in young pigs, Physiol. Behav. 43 (1988) 99–109.

[3] Black J.L., Mullan B.P., Lorschy M.L, Giles L.R., Lactation in the sow during heat stress, Livest. Prod. Sci. 35 (1993) 153–170.

[4] Castonguay T.W, Kaiser L.L., Stern J.S., Meal pattern analysis: artifacts, assumptions and implications, Brain Res. Bull. 17 (1986) 439–443.

[5] Collin A., van Milgen J., Dubois S., Noblet J., Effect of high temperature on feeding behaviour and heat production in grouped housed piglets, Brit. J. Nutr. 34 (2001) 279–290.

[6] Dagnelie P., Théorie et méthodes statistiques : applications agronomiques, Vol. 2, Les presses agronomique de Gembloux, Belgique, 1986.

[7] de Castro J.M., Meal pattern correlation: facts and artifacts, Physiol. Behav. 15 (1975) 13–15.

[8] de Castro J.M., The meal patterns of rats shifts from postprandial regulation to preprandial regulation when only five meals per day are scheduled, Physiol. Behav. 43 (1988) 739–746.

[9] de Haer L.C.M., Merks J.W.M., Patterns of daily food intake in growing pigs, Anim. Prod. 54 (1992) 95–104.

[10] de Vries J., Strubbe J.H., Wildering W.C., Gorter J.A., Prins J.A., Patterns of body temperature during feeding in rats under varying ambient temperature, Physiol. Behav. 53 (1993) 229–235.

[11] Dourmad J.Y., Standing and feeding behaviour of the lactating sow: effect of feeding level during pregnancy, Appl. Anim. Behav. Sci. 37 (1993) 311–319.

[12] Ermer P.M., Tilton S.L., Miller E.R., Lewis A.J, Wolverton C.K., The effect of dietary tallow on feed intake, meal patterns and fasting hormones

and metabolites in lactating sows, J. Anim. Sci. 73 (1995) 73.

[13] Hsia L.C., Wood-Gush D.G.M., A note on social facilitation and competition in the feeding behaviour of pigs, Anim. Prod. 37 (1983) 149–152.

[14] Labroue F., Aspect génétique du comportement alimentaire chez le porc en croissance, Thèse, École Nationale Supérieure d'Agriculture de Rennes, 1996.

[15] Labroue F., Guéblez R., Sellier P., Meunier-Salaün M.C., Feeding behaviour of group-housed Large White and Landrace pigs in French central test stations, Livest. Prod. Sci. 40 (1994) 303–312.

[16] Le Bellego L., van Milgen J., Dubois S., Noblet J., Energy utilization of low protein diets in growing pigs, J. Anim. Sci. 79 (2001) 1259–1271.

[17] Lynch P.B, Effect of environmental temperature on lactating sows and their litter, Irish J. Anim. Res. 16 (1977) 123–130.

[18] Montgomery G.W., Flux D.S., Carr J.R., Feeding patterns in pigs: the effect of amino acid deficiency, Physiol. Behav. 20 (1978) 693–698.

[19] Nienaber J.A., Hahn G.L., Korthals R.L., McDonald T.P., Eating behavior of swine influenced by environmental temperature, Trans. ASAE 36 (1993) 937–944.

[20] Nienaber J.A., Hahn G.L., McDonald T.P., Korthals R.L., Feeding patterns and swine performance in hot environments, Trans. ASAE 39 (1996) 195–202.

[21] Noblet J., Shi X.S., Dubois S., Energy cost of standing activity in sows, Livest. Prod. Sci. 34 (1993) 127–136.

[22] Noblet J., Fortune H., Shi X.S., Dubois S., Prediction of net energy value of feeds for growing pigs, J. Anim. Sci. 72 (1994) 344–354.

[23] NRC, Nutrient Requirement of Swine (tenth edition), National Academy Press, Washington, DC, 1998.

[24] Prunier A., Messias de Bragança M., Le Dividich J., Influence of high ambient temperature on performance of reproductive sows, Livest. Prod. Sci. 52 (1997) 123–133.

[25] Quiniou N., Noblet J., Influence of high ambient temperatures on performance of multiparous lactating sows, J. Anim. Sci. 77 (1999) 2124–2134.

[26] Quiniou N., Renaudeau D., Dubois S., Noblet J., Influence of high ambient temperatures on feed intake and feeding behaviour of multiparous lactating sows, Anim. Sci. 70 (2000) 471–479.

[27] Quiniou N., Renaudeau D., Dubois S., Noblet J., Effect of diurnally fluctuating high ambient temperatures on performance and feeding behaviour of multiparous lactating sows, Anim. Sci. 71 (2000) 571–575.

[28] Quiniou N., Dubois S., Noblet J., Voluntary feed intake and feeding behaviour of group-housed growing pigs are affected by ambient temperature and body weight, Livest. Prod. Sci. 63 (2000) 245–253.

[29] Quiniou N., Renaudeau D., Collin A., Noblet J., Effets de l'exposition au chaud sur les caractéristiques de la prise alimentaire du porc à différents stades physiologiques, INRA Prod. Anim. 13 (2000) 233–245.

[30] Renaudeau D., Noblet J., Effects of exposure to high ambient temperature and dietary protein level on sow milk production and performance of piglets, J. Anim. Sci. 79 (2001) 1540–1548.

[31] Renaudeau D., Quiniou N., Noblet J., Effects of exposure to high ambient temperature and dietary protein level on performance of multiparous lactating sows, J. Anim. Sci. 79 (2001) 1240–1249.

[32] SAS, SAS/STAT User's Guide (version 6, 4th ed.), SAS Inst. Inc., Cary, NC, 1998.

[33] Schoenherr W.D., Stahly T.S., Cromwell G.L., The effects of dietary fat or fiber addition on energy and nitrogen digestibility in lactating, primiparous sows housed in a warm or hot environment, J. Anim. Sci. 67 (1989) 473–481.

[34] Stahly T.S., Cromwell G.L., Aviotti M.P., The effect of environmental temperature and dietary lysine source and level on the performance and carcass characteristics of growing swine, J. Anim. Sci. 49 (1979) 1242–1251.

[35] Weldon W.C., Lewis A.J., Louis G.F., Kovar J.L., Giesemann M.A., Miller P.S., Postpartum hypophagia in primiparous sows: I. Effects of gestation feeding level on feed intake, feeding behavior, and plasma metabolite concentrations during lactation, J. Anim. Sci. 72 (1994) 387–394.

[36] Young R.J., Lawrence A.B., Feeding behavior of pigs in groups monitored by a computerized feeding system, Anim. Prod. 58 (1994) 145–152.