Chronic stress parameters in pigs

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Chapter 7

Effects of Nutritional Level on Body Temperature, Heart Rate and Behaviour in Growing Pigs

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Submitted.
ABSTRACT

Changes in body temperature, heart rate, salivary cortisol levels and behaviour are frequently measured as indicators of stress in growing pigs. The aim of the present experiment was to study the effects of the nutritional level on these parameters. Pigs were subjected to two treatments. One group of pigs (n=12) was first fed restricted from 42 until 84 days of age (at 70% of the average daily energy intake of a pig on that particular age), followed by ad libitum feeding. The other group of pigs (n=6) was continuously fed ad libitum. We showed that ad libitum fed pigs have a higher body temperature and heart rate than restricted fed pigs. No circadian body temperature rhythm was observed in restricted nor in ad libitum fed pigs. The circadian rhythm in heart rate disappeared when restricted fed pigs were given the opportunity to eat ad libitum, but was again observed after five days of ad libitum feeding. The nutritional level did not have an effect on the baseline salivary cortisol concentrations during the light period. Ad libitum fed pigs were less active and spent more time at the feeder than restricted fed pigs. The increased body temperature and heart rate in ad libitum fed pigs as compared to restricted fed pigs could be explained by an increased metabolic rate and increased heat production in ad libitum fed pigs, due to higher food intake and more frequently occurring feeding episodes. The effects of the nutritional level on physiology and behaviour are discussed in relation to pig welfare and health.
INTRODUCTION

The nutritional level may have an effect on the level of deep body temperature and the circadian rhythm in body temperature in growing pigs. Many years ago, few reports described the effects of food intake and fasting on the circadian variations in deep body temperature in growing pigs (Ingram and Legge, 1970; Ingram and Mount, 1973). During fasting, body temperature decreased, whereas during ad libitum feeding body temperature increased as compared to restricted feeding. No circadian body temperature rhythm was observed in pigs, and the body temperature variations were related to feeding, activity and sleep (Ingram and Legge, 1970; Ingram and Mount, 1973). More recently, it was suggested that a circadian rhythm in deep body temperature exists in restricted fed pigs, independent of feeding or activity (Parrott et al., 1998). Recent studies mentioned that piglets on a low nutritional level have a lower rectal temperature than piglets on a high nutritional level (Swiergiel, 1998; Rantzer et al., 1996), which seems to support previous findings that the nutritional level may affect the level of deep body temperature in growing pigs (Ingram and Legge, 1970; Ingram and Mount, 1973). In addition to these experiments, we (De Jong et al., 1999; De Jong et al., unpublished data) observed that ad libitum fed prepubertal pigs did not display a circadian rhythm in deep body temperature, and that the deep body temperature remained at a high level during the light and dark period (± 39.8°C-40.2°C).

Body temperature can be used as an indicator of health, but also as a physiological indicator of stress. In many species, it has been shown that deep body temperature increased in response to psychological stressors (stress-induced hyperthermia) (e.g. De Jong et al., 1998, 1999; Kluger et al., 1987; Parrott and Lloyd, 1995; Tornatzky and Miczek, 1993). Not only the body temperature level, but also the circadian rhythm in body temperature may change in response to stressors. It has been shown that the amplitude of the circadian rhythm in body temperature is decreased for days when rats were subjected to a single or repeated psychological stressor (Kant et al., 1991; Meerlo et al., 1996; Tornatzky and Miczek, 1993). If the nutritional level has an effect on the level of deep body temperature and the circadian rhythm in body temperature, than this should be taken into account when measuring (long-term) body temperature responses of pigs.
to stress. Therefore, we studied if restricted and *ad libitum* fed pigs differed in the level of deep body temperature and the circadian rhythm in body temperature.

As to the author's knowledge, the effect of the nutritional level on the level of heart rate and the circadian rhythm in heart rate in pigs has not been described yet. Heart rate is frequently measured in response to stressors (e.g. De Jong et al., 1998), and the circadian rhythm in heart rate may also change during stress (Tornatzky et al., 1998). Therefore, we also studied the effect of the nutritional level on heart rate. Deep body temperature and heart rate were measured by means of a biotransplant in freely moving pigs. To determine if changes in heart rate or body temperature at different nutritional levels were related to changes in activity level, the behaviour was also observed. In addition, baseline salivary cortisol concentrations were measured during the light period.

**MATERIALS AND METHODS**

All experiments were approved by the ID-Lelystad Animal Care and Use Committee (Lelystad, The Netherlands).

**Animals and Housing**

Eighteen crossbred gilts (Great Yorkshire x (Great Yorkshire x Dutch Landrace)) were used in the experiment. Gilts were randomly selected at weaning (28 days of age) and housed pairwise with a companion gilt from the same litter. At 35 days of age, gilts were transported to the experimental farm of the Institute for Animal Science and Health, Lelystad, The Netherlands. After arrival, gilts were housed pairwise with their companion gilts in pens (1.2 x 2.5 m) with half wooden floor covered with straw and half plastic slats. Two feed troughs were available per pen. Pens were cleaned daily at 08.00 h and fresh straw was provided. Pens were in climate-controlled rooms. Mean environmental temperature was 20.2°C, and additional heating using a heating lamp in the pens was provided until 49 days of age. Lights were on from 06.00 – 18.00 h; no daylight was visible in the rooms. Water was available *ad libitum*.

**Feeding Regime**

Pigs were subjected to two different feeding regimes. One group of gilts (RF group, n=12) was subjected to a restricted feeding regime from 42 days of age
followed by *ad libitum* feeding from 84 days of age. During the period of restricted feeding, energy intake was limited to 90% of the average daily intake of a pig at 42-49 days of age, to 80% at 49-56 days of age, and to 70% at 56-84 days of age. During the period of restricted feeding, pigs were fed twice a day at 08.00 h and 15.00 h. In each pen two feed troughs were present; in one trough food for one pig was supplied. From 84 to 105 days of age pigs were fed *ad libitum*; food was provided once a day at 08.00 h. The second treatment group (AL group; n=6) was fed *ad libitum* until the end of the experiment (105 days of age). For the AL pigs, food was provided at 08.00 h. Companion pigs received the same feeding regime as the experimental pigs.

**Surgery**

Transmitters measuring body temperature and heart rate were implanted under complete anesthesia at 61 days of age as described elsewhere (De Jong et al., 1998). Pigs were sedated with ketamine (15 mg/kg i.m., Nimatek®, AUV, Cuijck, The Netherlands) and subsequently anesthetised using midazolam (1.5 mg/kg i.v., Dormicum®, Roche, Mijdrecht, The Netherlands). Transmitters were implanted intraperitoneally. Electrode leads were extended subcutaneously and sutured caudal and cranial to the thorax. Pigs were treated with antibiotics (Ampicillan 20%®, AUV) during 5 days after implantation.

**Weight Development**

Pigs were weighed at weaning (28 days of age), at arrival at the experimental farm (35 days of age), and in addition at 42, 70, 84 and 105 days of age.

**Physiological and Behavioural Measurements**

Body temperature, heart rate and salivary cortisol concentration were measured and the behaviour was observed at the end of the restricted feeding period for the RF pigs and during the *ad libitum* feeding period for the RF pigs. For the AL pigs, parameters were measured at the same time points.

**Body Temperature and Heart Rate Measurements**

Body temperature and heart rate were measured during 17 days between 79 and 96 days of age by means of radiotelemetry using implantable biotelemetric transmitters (type TA10CTA-D70, DataSciences, St Paul, MN, USA), as described
elsewhere (De Jong et al., 1998). Receivers (type RLA2000, DataSciences) were connected to a multiplexer (RMX10, DataSciences) and subsequently to a matrix (BCM100, DataSciences) routing the signal to a personal computer containing the LabPro analysis software (version 3.11, DataSciences) for analysis of the data. Body temperature and heart rate were measured during 5 days of the restricted feeding period and during 12 days of the *ad libitum* feeding period for the RF pigs, and during the same time span for the AL pigs.

**Saliva Collection and Cortisol Analysis**

Saliva was collected every hour during the light period (6.00-18.00 h) at 82 days of age (restricted feeding) and at 95 days of age (*ad libitum* feeding) for the RF pigs, and at the same time points for the AL pigs. Saliva was collected by allowing the pigs to chew on two large cotton buds until they were thoroughly moistened (about 30-60 sec per sample). The buds were placed in tubes and centrifuged for 10 min at 400 g. Saliva samples were stored at −20°C until analysis. Cortisol concentration in saliva samples was determined using a solid-phase radioimmunoassay kit (Coat-a-Count Cortisol TKCO, Diagnostics Product Corporation, Apeldoorn, The Netherlands) modified for pig salivary cortisol (Ruis et al., 1997). Cortisol in saliva is a good representation of the level in plasma and is essentially in the free biologically active form (Kirschbaum and Hellhammer, 1989).

**Behavioural Observations**

Behaviour was recorded on videotape during the light period (6.00-18.00 h) on 2 days of the restricted feeding period (80-81 days of age) and on 2 days of the *ad libitum* feeding period (93-94 days of age) for the RF pigs, and at the same time points for the AL pigs. Duration and frequency of the behavioural elements as described in Table 1 were scored continuously per pig using the Observer software (Noldus, Wageningen, The Netherlands).
Table 1. Ethogram

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eating</td>
<td>Time spent with the head in the feeder</td>
</tr>
<tr>
<td>Drinking</td>
<td>Time spent drinking</td>
</tr>
<tr>
<td>Walking</td>
<td>Walking through the pen</td>
</tr>
<tr>
<td>Running</td>
<td>Trotting, galloping through the pen</td>
</tr>
<tr>
<td>Explore pen</td>
<td>Rooting, sniffing or touching the walls or ground of the pen or feeder</td>
</tr>
<tr>
<td></td>
<td>(without eating), except substrate</td>
</tr>
<tr>
<td>Explore straw</td>
<td>Rooting, sniffing, touching the substrate</td>
</tr>
<tr>
<td>Nosing</td>
<td>Sniffing with the nose any part of another pig</td>
</tr>
<tr>
<td>Fighting</td>
<td>Agonistic interactions with biting involved</td>
</tr>
<tr>
<td>Other</td>
<td>All other behaviour</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Posture</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standing</td>
<td>Standing, walking, running on four legs</td>
</tr>
<tr>
<td>Lying</td>
<td>Lying on side or sternum</td>
</tr>
<tr>
<td>Sitting</td>
<td>Standing on fore-legs, hind quarter on the floor</td>
</tr>
</tbody>
</table>

Data Reduction and Statistical Analysis

Body temperature and heart rate levels were compared between the restricted feeding period and the *ad libitum* feeding period by calculating the body temperature and heart rate average of 79-84 days of age (restricted feeding for the RF pigs) and of 84-96 days of age (*ad libitum* feeding for the RF pigs). In addition, body temperature and heart rate data were averaged over the 12-hour light and dark phases. The amplitude of the circadian rhythm was defined as the difference between an average light value and an average dark value.

Growth of the pigs and energy intake were compared between RF and AL pigs using a mixed analysis of variance model with treatment (RF vs. AL) as fixed effect in the model and the animal entered as random effect. Components were estimated with the Restricted Maximum Likelihood (REML) procedure (Genstat, 1993). The residuals were checked for homogeneity of variance. Salivary cortisol concentrations, behaviour, average values of body temperature and heart rate, and amplitude values were compared between RF and AL pigs, and within animals between different ages, with the Mann-Whitney U test. Differences were significant if p<0.05.
RESULTS

Energy Intake, Growth Rate and Weight

During the period of restricted feeding, energy intake of the RF pigs was significantly lower (p<0.0001; Table 2) than energy intake of the AL pigs. Energy intake of the RF pigs during the period of restrictive feeding decreased from 81% to 48% of the energy intake of the AL pigs (Table 2). Thus, in this experiment AL pigs consumed more food than expected, as the food restriction for the RF pigs was more than 70% of the intake of the AL pigs. However, when the RF pigs were given the opportunity to eat *ad libitum* after the period of restricted feeding, energy intake did not differ significantly between RF and AL pigs (Table 2).

As a consequence, AL pigs had a higher growth rate from 42 to 84 days of age than RF pigs (Table 3). When the RF pigs were given the opportunity to eat *ad libitum* after 84 days of age, they had a significantly higher growth rate than the AL pigs (Table 3). At weaning and at 35 days of age, AL pigs weighed slightly but significantly more than RF pigs (28 days of age: 8.3 ± 0.2 kg vs. 8.6 ± 0.2 kg for RF vs. AL pigs, p<0.05; 35 days of age: 9.2 ± 0.3 vs. 10.2 ± 0.5 kg for RF pigs vs. AL pigs, p<0.05). At 42 days of age, AL and RF pigs did not differ in weight. At 70, 84 and 105 days of age AL pigs weighed significantly more than RF pigs (70 days of age: 21.8 ± 0.4 kg vs. 28.5 ± 1.2 kg for RF vs. AL pigs, p<0.001; 84 days of age: 25.7 ± 0.5 kg vs. 39.0 ± 1.5 kg for RF pigs vs. AL pigs, p<0.001; 105 days of age: 47.7 ± 0.7 kg vs. 55.5 ± 2.3 kg for RF pigs vs. AL pigs, p<0.001).
Table 2. Daily energy intake (kJ) for the RF pigs and the AL pigs.

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>Mean daily energy intake per pig (kJ)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RF pigs</td>
</tr>
<tr>
<td>35-42</td>
<td>4052$^a$</td>
</tr>
<tr>
<td>42-49</td>
<td>5577</td>
</tr>
<tr>
<td>49-56</td>
<td>6106</td>
</tr>
<tr>
<td>56-63</td>
<td>6902</td>
</tr>
<tr>
<td>63-70</td>
<td>7592</td>
</tr>
<tr>
<td>70-77</td>
<td>7611</td>
</tr>
<tr>
<td>77-84</td>
<td>8303</td>
</tr>
<tr>
<td>84-91</td>
<td>16937$^a$</td>
</tr>
<tr>
<td>91-98</td>
<td>20149$^a$</td>
</tr>
<tr>
<td>98-105</td>
<td>23509$^a$</td>
</tr>
</tbody>
</table>

$^a$ Ad libitum feeding at this age. Energy intake represents the mean daily intake of all pigs (experimental pigs and companion pigs; n=24).

$^b$ Energy intake represents the mean daily intake of all pigs (experimental pigs and companion pigs; n=12).

$^c$ p<0.0001; AL pigs vs. RF pigs

Table 3. Growth (mean ± sem) for the RF and the AL pigs

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>Growth (kg/week)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RF pigs</td>
</tr>
<tr>
<td>28-35</td>
<td>0.96 ± 0.16$^c$</td>
</tr>
<tr>
<td>35-42</td>
<td>1.97 ± 0.17$^a$</td>
</tr>
<tr>
<td>42-70</td>
<td>2.63 ± 0.08</td>
</tr>
<tr>
<td>70-84</td>
<td>1.84 ± 0.12</td>
</tr>
<tr>
<td>84-105</td>
<td>7.60 ± 0.29$^a$</td>
</tr>
</tbody>
</table>

$^a$Ad libitum feeding at this age

Body Temperature

Although pigs of the AL group had a higher average body temperature from 79-84 days of age than pigs of the RF group (39.76 ± 0.03°C vs. 39.53 ± 0.06°C for AL pigs vs. RF pigs), differences were not significant. The average body temperature did not differ between pigs of the AL group and pigs of the RF group.
between 84-96 days of age, when both groups were fed *ad libitum* (39.77 ± 0.01°C vs. 39.84 ± 0.04°C for AL pigs vs. RF pigs).

Pigs that were first fed restricted followed by *ad libitum* feeding (RF pigs), showed an increase in body temperature from the moment of *ad libitum* feeding (Figure 1). Average body temperature during the period of *ad libitum* feeding was significantly higher than the average body temperature during the period of restricted feeding (p<0.001). AL pigs did not differ significantly in the average body temperature between 79-84 and 84-96 days of age.

When the body temperature was averaged over the 12 h light and dark period (Figure 1), no circadian body temperature rhythm entrained to the light/dark cycle could be observed in restricted nor in *ad libitum* fed pigs.

Figure 1. 12-hour body temperature averages of the light and dark period of pigs of the RF group and the AL group from 79 to 96 days of age. RF pigs were fed restricted from 79 to 84 days of age.
Heart Rate

When heart rates were compared between AL and the RF pigs of the same age, the average heart rate from 79-84 days of age was significantly higher for the AL pigs than for the RF pigs (125.9 ± 2.3 bpm vs. 112.8 ± 2.6 bpm for AL pigs vs. RF pigs; p<0.01). From 84-96 days of age, RF pigs had a significantly higher average heart rate than the AL pigs (137.7 ± 1.8 bpm vs. 116.2± 0.9 bpm for RF pigs vs. AL pigs; p<0.001).

Pigs that were first fed restricted followed by ad libitum feeding (RF pigs), had a significantly lower average heart rate during the period of restricted feeding than during the period of ad libitum feeding (p<0.01; Figure 2). Heart rate during the period of restricted feeding showed a clear circadian rhythm entrained to the light/dark period, with a high heart rate during the light period and a low heart rate during the dark period. Heart rate increased immediately after the start of ad libitum feeding. The circadian rhythm in heart rate disappeared for several days when the pigs were fed ad libitum, but appeared again after five days of ad libitum feeding (Figure 2).

For the AL pigs, heart rate decreased slightly between 79 and 96 days of age. When the average heart rate was compared for the same time span as for the RF group, data showed that the AL group had a significantly lower heart rate from 84-96 days of age than from 79-84 days of age (p<0.05). AL pigs displayed a circadian rhythm in heart rate entrained to the light/dark cycle (Figure 2).

The amplitudes of the heart rate rhythm during the ad libitum feeding period of the RF pigs seems to be smaller than during the restricted feeding period of the RF pigs, and seems to be smaller than the heart rate amplitude of the AL pigs (Figure 2). However, when the amplitudes of the heart rate rhythm were compared between pigs that were fed restricted or ad libitum, no significant differences were found.
Figure 2. 12-hour heart rate averages of the light and dark period of pigs of the RF group and the AL group from 79 to 96 days of age. RF pigs were fed restricted from 79 to 84 days of age.

**Behaviour**

At 80-81 days of age, RF pigs that were restricted fed largely differed in their behaviour from AL pigs (Figure 3a). RF pigs spent significantly more time standing (p<0.001), walking (p<0.001), exploring the pen (p<0.001) and exploring the substrate (p<0.001). In addition, RF pigs spent significantly less time lying (p<0.001), being inactive (p<0.001) and eating (p<0.01) than AL pigs. At 93-94 days of age, when both RF pigs and AL pigs were fed *ad libitum*, RF pigs spent more time eating than AL pigs (p<0.05). RF pigs did not differ significantly from AL pigs in time spent on other behavioural elements at this age (Figure 3b).

RF pigs also differed from AL pigs in the frequency of changing the position during the period of restricted feeding. The frequency of standing, lying and sitting was significantly lower for RF pigs than for AL pigs at 80-81 days of age.
(standing: 35.7±4.2 vs. 61.6±7.4, p<0.05; lying 36.1±4.8 vs. 68.6±8.2, p=0.01; sitting 18.8±3.0 vs. 51.2±6.3, p<0.001 for RF pigs vs. AL pigs). At 93-94 days of age during the period of *ad libitum* feeding for the RF pigs, RF pigs and AL pigs did not differ in the frequency of standing and lying (standing: 56.2±3.6 vs. 65.6±11.6, n.s.; lying: 59.1±3.2 vs. 77.6±12.1, n.s. for RF pigs vs. AL pigs). However, the frequency of sitting was significantly higher for the AL pigs than for the RF pigs at 93-94 days of age (32.9±3.6 vs. 61.9±6.6, p<0.001 for RF pigs vs. AL pigs).

Pigs from the RF group differed in their behaviour during the period of restricted feeding (80-81 days of age) as compared to the period of *ad libitum* feeding (93-94 days of age). When restricted fed, pigs of the RF group spent significantly more time standing (p<0.001), exploring the pen (p<0.01) or exploring straw (p<0.01), and less time on lying (p<0.001), eating (p<0.05) and being inactive (p<0.001) than when *ad libitum* fed. Pigs from the AL group did not significantly differ in their behaviour at 80-81 days of age when compared to 93-94 days of age. Pigs from the RF group also differed in the frequency of standing, lying and sitting during the period of restricted feeding as compared to the period of *ad libitum* feeding. When restricted fed, the frequency of standing (p<0.01), lying (p<0.01) and sitting (p<0.001) was significantly lower than when *ad libitum* fed. Pigs from the AL group did not differ in the frequency of standing, lying and sitting at 81-81 days of age as compared to 93-94 days of age.

**Cortisol**

At 82 days of age, RF pigs, that were fed restricted, had a significantly higher cortisol concentration than AL pigs at 14.00 h (p<0.05; Figure 4a). The salivary cortisol concentration did not differ between RF pigs and AL pigs at all other time points. At 95 days of age, when both RF and AL pigs were fed *ad libitum*, salivary cortisol concentrations did not differ significantly between both treatments (Figure 4b).

Pigs of the RF group had a significantly higher salivary cortisol concentration at 10.00 h (p<0.05) and at 14.00 h (p<0.01) at 82 days of age, when they were fed restricted, as compared to 95 days of age when they fed *ad libitum*. Salivary cortisol concentrations at other time points did not differ between RF pigs at 82 and 95 days of age. Pigs of the AL group did not differ in their salivary cortisol concentration at all time points between 82 and 95 days of age.
Figure 3. Behaviour of RF pigs and AL pigs at A. 80-81 days of age and B. 93-94 days of age. *p<0.05; **p<0.01; ***p<0.001. sta=standing; ly=lying; sit=sitting; eat=eating; dr=drinking; inact=inactive; walk=walking; run=running; exp=exploring pen; exs=exploring substrate; nose=nosing; figh=fighting; oth=other.
Figure 4. Salivary cortisol concentration during the light period (6.00 h - 18.00 h) of RF and AL pigs at A. 82 days of age and B. 95 days of age. *p<0.05.
DISCUSSION

The principal findings of this experiment were that prepubertal pigs that are fed *ad libitum* have a higher body temperature, a higher heart rate and are less active than restricted fed pigs. Salivary cortisol levels during the light period were not affected by the nutritional level.

The results of the present experiment confirm previous studies, that suggested that piglets fed on a low nutritional level have a lower body temperature than piglets fed on a high nutritional level (Ingram and Mount, 1973; Swiergiel, 1998; Rantzer et al., 1996). During feeding, the sympathetic nervous system is increasingly activated, and heat production and body temperature increase (Himms-Hagen, 1995; Rothwell and Stock, 1983; Van der Hel et al., 1984). The increased body temperature of *ad libitum* fed pigs as compared to restricted fed pigs can be explained by an increased heat production due to an increased food intake, and more frequently occurring feeding episodes. Moreover, it has been shown that rodents and men are able to compensate for excessive energy intake by increasing energy expenditure, which is accompanied by an increased body temperature (Rothwell and Stock, 1983). This mechanism may also play a role in *ad libitum* fed growing pigs.

Previous reports on the occurrence of a circadian body temperature rhythm in pigs are contradictory. Parrott et al. (1998) observed that a circadian rhythm in body temperature was present in restricted fed pigs, with a rise in body temperature during the afternoon. Becker et al. (1997) observed a body temperature rhythm in *ad libitum* fed pigs, with highest body temperatures during the dark period. However, others suggested that pigs do not display a circadian rhythm in body temperature (Ingram and Legge, 1970; Ingram and Mount, 1973). The most important 'zeitgeber' for synchronisation of the circadian clock is the daily light/dark cycle (Beersma and Hiddinga, 1998). We showed that both *ad libitum* and restricted fed pigs did not have a circadian body temperature rhythm entrained to the light/dark cycle, confirming the results of Ingram and Mount (1973) and Ingram and Legge (1970).

It has been shown that *ad libitum* fed pigs eat during the dark period as well as during the light period (Musial et al., 1999). It can therefore be expected that nocturnal food intake may mask the circadian body temperature rhythm in these pigs, because heat production and body temperature increase due to feeding
(Heetkamp et al., 1995; Himms-Hagen, 1995; Van der Hel et al., 1984). In restricted fed pigs, it has been shown that heat production shows a circadian rhythm, that is related to the feeding episodes in the light period (Heetkamp et al., 1995; Van der Hel et al., 1984). However, we did not observe a circadian rhythm in body temperature in restricted fed pigs, whereas a higher body temperature in the light period than in the dark period could be expected because of the increased heat production due to feeding in the light period. Thus, the absence of a circadian body temperature rhythm during restricted feeding is due to other, unknown factors. It may be possible that the circadian body temperature rhythm will develop at a later age because we studied prepubertal growing pigs, however, it has been shown in humans and rodents that circadian rhythms in body temperature are already present at a young age (e.g. McGraw et al., 1999; Nuesslein and Schmidt, 1990).

We observed that ad libitum fed pigs have a higher mean heart rate than restricted fed pigs, which can be explained by more frequently occurring feeding episodes in ad libitum fed pigs, and a higher metabolism due to the increased food intake. A decreasing heart rate with age was observed in AL pigs. Although the total energy intake increased slightly in the AL pigs, the increase per kg metabolic weight decreased with age which may explain the decreasing heart rate.

Both ad libitum and restricted fed pigs displayed a circadian rhythm in heart rate entrained to the light/dark cycle. This can be explained by a higher food intake and thus a higher metabolic rate, and a higher activity level during the day than during the night (Van der Hel et al., 1984). The amplitude of the circadian rhythm in heart rate tends to be smaller in ad libitum fed pigs than in restricted fed pigs, which may be due to nocturnal feeding. When restricted fed pigs are given the opportunity to eat ad libitum, the circadian rhythm in heart rate disappears during several days. This may be due to the large increase in (nocturnal) food intake after food restriction, and as a consequence a large increase in metabolism.

Behavioural observations showed that ad libitum fed pigs are less active than restricted fed pigs during the light period. In addition, the frequency of changing the position was higher in ad libitum fed pigs as compared to restricted fed pigs. This indicates that ad libitum fed pigs show active behaviour during frequent short periods, whereas restricted fed pigs show active behaviour during several long periods. Body temperature and heart rate increase with increasing activity. In ad libitum fed pigs activity may be limited to short periods as a way of thermoregulation, to prevent thermal discomfort. RF pigs could also be more active
during the restricted feeding period because they were hungry and searched for food. However, the restricted fed pigs consumed enough energy for maintenance and moderate growth. The frequency of sitting was significantly higher in pigs of the AL group than in pigs of the RF group at both time points. This may indicate that AL pigs, that weighed more, may have problems with changing the position. Selection of pigs for high growth rate caused leg weakness (Rauw et al., 1998), which may become apparent in the heavier AL pigs.

The higher salivary cortisol concentration at 14.00 h in restricted fed pigs than in ad libitum fed pigs may represent the prefeeding peak in corticosterone (e.g. Honma et al., 1986), because RF pigs were fed at 15.00 h. Salivary cortisol concentrations did not differ between restricted and ad libitum fed pigs at other time points, which confirmed a previous experiment in weaned piglets (Rantzer et al. 1996). This may indicate that moderate food restriction does not subject the pigs to a situation of stress. However, during chronic stress changes may occur at different levels of the HPA-axis (Jensen et al., 1996), which remains to be investigated in restricted fed pigs.

It can be questioned whether pigs should be fed restricted or ad libitum with respect to welfare and health. Swiergiel (1998) states that with respect to welfare, precise body temperature regulation by food intake is important for pigs, thus, ad libitum feeding should be preferred. However, ad libitum fed pigs have a very high food intake. Studies in humans and rodents showed that chronic nutritional excess is a risk factor for hypertension, cancer, cardiovascular disease and metabolic abnormalities (Scheurink et al., 1996; Woods, 1991). Thus, a chronic high nutritional level may eventually lead to health problems in fattening pigs. It has been shown that pigs selected for high skeletal muscularity have a higher risk for impaired heart function (Geers et al., 1990) and cardiac hypertrophy (Yang and Lin, 1997). This may also have been caused by the high food intake in these pigs. Because fattening pigs are slaughtered before reaching puberty, health problems may not always become apparent. It may also be expected that pigs that have higher heart rates and body temperature and that are less active may have problems to cope with physical and psychological stressors as compared to pigs fed on a lower nutritional level, because body temperature and heart rate may reach high levels due to stress (e.g. see De Jong et al., 1998, 1999; Parrott and Lloyd, 1995). More research will be necessary to study the effects of the nutritional level on welfare and health of fattening pigs.
In conclusion, we showed that the nutritional level affects baseline body temperature, heart rate and home pen behaviour, and may probably also affect physiological and behavioural stress responses, and thus may have an effect on pig welfare and health. Therefore, when measuring stress responses, the nutritional level of pigs should be taken into account. In addition, one should be careful to compare physiological and behavioural stress responses between ad libitum fed pigs and restricted fed pigs.

REFERENCES


