

MOTIVATED FOR MOVEMENT? EXERCISE AND THE GESTATION ENVIRONMENT
ON SOW PERFORMANCE AND WELFARE

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ABSTRACT

The societal concern regarding sow confinement has prompted multiple countries to move towards providing a greater freedom of movement to gestating sows. The 2014 Canadian Code of Practice for the Care and Handling of Pigs permits the operation of existing stall barns if bred female pigs are given access to periodic exercise. The objective of this thesis was to determine how strongly gestating female pigs are motivated for time out of their stall, and if providing periodic exercise can increase sow welfare and reduce stress in comparison to housing in stalls and groups throughout gestation. Chapter 3 compared gilt and sow motivation for movement and food using an operant panel. In Chapter 4, operant panel testing was used to compare motivation to exit the stall in sows at three levels of satiety achieved by feeding high fibre (HF) feed. Finally, the welfare (Chapter 5) and productivity (Chapter 6) of gestating sows receiving exercise (E; walking/running 160 m/week) vs sows housed in stalls (C) and groups (G) during pregnancy was evaluated. Chapter 3 found that both gilts and sows demonstrated that they were equally motivated to exit the stall, and sows were more motivated for food than gilts. Chapter 4 found that feed restricted sows were more motivated for movement than sows fed HF ad-lib, with sows receiving 50% of their ad-lib HF intake being intermediate. Chapter 5 found that G sows lay more, sat less and performed fewer stereotypies than C and E sows. Chapter 6 found that in parities 5-7 E and G sows had a greater number of liveborn than C sows. These results suggest that gestating female pigs are motivated for movement, and this motivation has a strong exploratory/foraging component. Group housing, but not periodic exercise improved sow comfort and reduced stress, as indicated by postures and stereotypies. Periodic exercise improved reproductive performance in older sows only. In conclusion, periodic exercise at a low level does not provide any welfare or production benefits. Whereas group housing was shown to better meet the needs of the sow than periodic exercise, and a transition to group-housing is advisable.

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LIST OF ABBREVIATIONS

°C	degree Celsius
AB	active button
ACTH	adrenocorticotrophic hormone
AICC	Akaike's information criterion corrected
AM	ante meridiem (before noon)
BCS	body condition score
BIC	Bayesian information criterion
BMI	body mass index
C	control (treatment)
CEC	Commission of the European Communities
CIWF	Compassion in World Farming (organization)
cm	centimeter
CO	Colorado
DB	dummy button
E	exercise (treatment)
EIA	enzyme immunoassay
ESF	electronic sow feeder
EU	European Union
Ex	exploratory behaviour
FAWC	Farm Animal Welfare Committee
Fig.	figure
FR	fixed ratio
g	gram
G	group (treatment)
h	hour
HF	high fibre
HPA	hypothalamus-pituitary-adrenocortical
HPLC	high-performance liquid chromatography
HPP	highest price paid

hrs	hours
Hz	Hertz
ICC	intraclass correlation coefficient
IgG	immunoglobulin G
IRR	intrarater reliability
IUGR	intrauterine growth restriction
kg	kilogram
L	locomotion
LED	light-emitting diode
m	meter
max	maximum
Mcal	megacalories
mg	milligram
min	minimum
mins	minutes
ml	milliliter
mm	millimeter
NAWAC	National Animal Welfare Advisory Committee
NC	North Carolina
NFACC	National Farm Animal Care Council
NK	natural killer
NY	New York
O	other behaviours
ON	Ontario
ONF	oral-nasal-facial
PA	Pennsylvania
pg	picogram
pg.	page
PI	ponderal index
PI	pulsatility index

PIC	Pig Improvement Company
PM	post meridiem (after noon)
PNS	prenatal stress
PSE	prior stall experience
PTE	prior training experience
PVC	polyvinyl chloride
RI	resistance index
rpm	revolutions per minute
r_s	Spearman's rank correlation coefficient
s	second
S	snout to snout contact
SAS	SAS Institute Inc.
SD	standard deviation
SEM	standard error of the mean
SNS	sympathetic nervous system
T	tendency
US	United States
USA	United States of America
vs	versus

1. INTRODUCTION

With gestation stalls remaining the most popular sow housing system in the world within intensive production systems, the effects of close confinement on the welfare of pregnant sows is a hot topic within societal debate about the pork industry. A US poll studying public views of an ideal pig farm (Sato et al., 2017) showed that housing pigs in confinement is the top public concern, mentioned by 44% of respondents. Another survey on gestating sow housing, which included Canadian and US participants revealed that 55.6% of respondents supported group housing, and among those 30.4% of respondents who originally supported the stall-housing system, 12.6% changed their mind in favour of group housing when provided with additional information about stall and group-housing systems (Ryan et al., 2015). Additionally, the comments received from respondents of the latter survey indicated the presence of strong concerns about sows' behavioural freedom in intensive housing systems, including giving sows opportunities for social interaction, movement and expressing natural behaviour.

In an effort to address the societal concern regarding keeping sows in stalls during gestation, numerous countries including the United Kingdom, Australia, New Zealand, the EU and several states in the USA enacted bans on the use of gestation crates and switched to group housing systems (Baxter et al., 2018). Aiming to improve sow welfare in confinement gestation housing conditions, the Canadian Code of Practice for the Care and Handling of Pigs Committee included a requirement to provide stall-housed gestating female pigs with a greater freedom of movement in the 2014 Code of Practice for the Care and Handling of Pigs. The Code states that all newly built barns must house sows in groups, but any barns built before July 1, 2014, can continue to house bred gilts and sows in stalls if they receive a greater freedom of movement (NFACC, 2014). This hybrid approach was taken due to concerns over the ability of the Canadian pork industry to make a conversion to the group-housing system within the allotted timeframe of 10 years. A public major concern of delaying the conversion to group sow housing is sows remaining in gestation stalls longer. This led to the proposition that alternative approaches to

providing a greater freedom of movement would be considered for sows remaining in stalls post 2024.

It is important to understand that policy changes designed to protect animal welfare can sometimes be driven by emotive arguments rather than by scientific evidence. Freedom of movement is one of the most basic animal welfare concerns; it is represented in the Five Freedoms concept of animal welfare by freedom to express normal behaviour (FAWC, 1993), and as previously demonstrated by public surveys, it is very important to pork consumers. In the case of gestation stalls, the mixed results of previous research demonstrated that both group and stall-housing systems have their pros and cons and that both of these systems can provide an acceptable level of welfare if managed properly (DeDecker, 2011). However, this is also dependent on where the values are placed: as stalls cannot provide freedom of movement, this housing option is unacceptable for some people. As the group-housing system for gestating sows is more societally acceptable, scientific evidence would support this system as well, if we can assure that the groups are well-managed.

Previous studies comparing housing systems with different levels of access to a greater freedom of movement (mostly groups vs stalls) looked primarily at physical, physiological and some behavioural measures of sow welfare, paying little attention to animal psychological well-being and affective states. However, it is important to understand how strongly sows value a greater freedom of movement and are motivated to access it. If having access to a greater freedom of movement is beneficial for a sow's physical health, but does not significantly improve or even worsens her mental condition, then the optimal levels of animal welfare will not be achieved and other options of enhancing gestating sow welfare should be looked into, especially considering that providing a greater freedom of movement is not a simple requirement to accommodate in commercial barn conditions. It also needs to be understood how important is providing a greater freedom of movement if it is the only change that is implemented to improve gestating sow housing.

It is also important to consider the economic implications of providing sows with a greater freedom of movement. While the conversion of stall barns to group-housing systems is expensive and estimated to increase pork production costs by 1-2 % (CIWF, 2014), providing sows with other options for a greater freedom of movement would also incur costs. Switching to systems such as turn-around stalls and width adjustable gestation crates would require

conversions of stall barns. Providing periodic exercise to gestating sows would require increased labour to release sows from stalls one at a time to prevent aggressive encounters. For example, it was estimated that a 1200-sow operation with gestating sows exercised once per week for 10 minutes (equivalent to walking sows for approximately 160 m) would require full-time labour from four additional people to exercise sows. Assuming an hourly labour rate is \$15, this change would result in additional \$127,400 spent on sow exercise per year (Tokareva et al., 2020).

Previous research showed some impact of intensive regimes of periodic exercise on sow physical, physiological and behavioural measures of welfare, such as improved bone strength, increased umbilical blood flow, reduced preweaning mortality and reduced restless behaviour (Schenck et al., 2008; Harris et al., 2013). However, it is not realistic to implement the levels of exercise used in the above-mentioned studies (at least three times/week for at least 30 mins) in commercial barns, due to tremendous increase in labour requirements. Providing sows with lower levels of exercise would more likely be achievable in commercial practice, but whether providing sows with exercise using low-intensity schedules could bring any benefits to sow welfare in comparison to group-housing and stall-housing without exercise, is currently unknown. Understanding if sows are motivated for having time out of the stall periodically would help to determine if periodic exercise could be beneficial for sow welfare. Additionally, the contributing factors of each housing system that could lead to production benefits need to be explored.

The central aim of this thesis was to determine through the measurement of sow motivation how important access to a greater freedom of movement is for gestating female pigs, and if providing periodic exercise can increase their welfare and reduce stress in comparison to housing in stalls throughout gestation and to housing in groups. To achieve this aim, four experiments were conducted. The first study covered in Chapter 3 explored whether stall-housed female pigs with or without previous stall experience (stall-experienced vs stall-naïve) are motivated to access time out of their stall, through comparing their motivation to leave the stall with their motivation to obtain a food reward. To better understand the factors influencing the motivation of sows to leave the stall and to confirm that sows are motivated to leave the stall not only due to their desire to find additional feed but also because of being motivated to exercise, the second study covered in Chapter 4 explored if the motivation of stall-housed gestating sows to leave their stall is influenced by sow satiety level. The third and fourth studies covered in Chapters 5

and 6 looked at the effects of providing periodic exercise at a low level, which is achievable in commercial barn settings (walking/running once a week for 160 m). The third experiment was designed to evaluate the welfare and stress physiology of stall-housed periodically exercised gestating sows in comparison to the sows stall-housed without exercise and group-housed sows; additionally, the piglet behavioural response to stress tests was compared across the treatments. This was done to understand whether the standard gestation environment in itself is stressful, and if so, how the other treatments compare to it. In this study, a novel measure of chronic gestational stress, hair cortisol, was introduced to help understand the levels of stress experienced by sows over the whole gestation period, as previous studies mainly focused on acute measures of stress, at mixing (for example Jansen et al., 2007). The fourth experiment was built upon the third study, and it looked at the effects of periodic exercise on such aspects of sow reproductive performance, placental development and piglet viability. This information would help to understand the mechanisms by which physical exercise affects gestating sows and their offspring, and also to make an informed decision on whether providing periodic exercise could potentially be commercially beneficial for the performance of the sow and piglets, and thus the efficiency of the swine production industry. This body of work will not only contribute information to the development of the Canadian Code of Practice for the Care and Handling of Pigs but will also help to advance our understanding of gestating sow welfare.

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2. LITERATURE REVIEW

2.1 Introduction

The welfare of gestating sows housed in stalls is a major topic of public concern regarding the pork industry (Schulz and Tonsor, 2015). Keeping sows in gestation stalls results in a conflict between sows' biological needs and housing design, and is criticized for compromising the welfare of female pigs (Baxter et al., 2018). This housing system has already been banned in numerous countries, and Canada is in the process of implementing changes to gestating sow housing in order to meet societal expectations.

Canada enacted changes to pregnant sow housing in the Code of Practice for the Care and Handling of Pigs in 2014. As required by the Code, "For all holdings newly built or rebuilt or brought into use for the first time after July 1, 2014, mated gilts and sows must be housed in groups. Individual stalls may be used for up to 28 days after the date of last breeding, and an additional period of up to 7 days is permitted to manage grouping," (NFACC, 2014, pg. 11). Any existing barns built prior to this date, and in good working order, can continue to house sows in stalls throughout gestation. However, to protect the welfare of sows continuing to be housed in gestation stalls the Code also states that "as of July 1, 2024, mated gilts and sows must be housed in groups, or in individual pens, or in stalls, if they are provided with the opportunity to turn around or exercise periodically, or other means that allow greater freedom of movement," (NFACC, 2014, pg.11).

Reviews of previous studies have found similar productivity, physiology, health and behaviour among sows housed individually or in groups during gestation (McGlone et al., 2004; Rhodes et al., 2005; McGlone, 2013). So the dispute about which housing system is better or worse for sow welfare continues, as there are tradeoffs with each system.

However, apart from the impact on the sow, the gestation housing system may also influence birth outcomes in sows and offspring characteristics, a result of repeated or a prolonged stress response to aversive environmental stimuli in gestating dams. It is considered

that gestational stress can have a significant impact on maternal reproductive performance, fetal development, birth weight, physiology and the behaviour of offspring (Patin et al., 2002; Jarvis et al., 2006). Multiple previous studies comparing the impact of gestation housing systems, primarily groups and gestation stalls, on different aspects of sow welfare found no difference in reproductive parameters (McGlone, 2013). But further investigation is needed to determine the relationship between the gestational stress experienced by sows under commercial swine production conditions and offspring characteristics, the development of which could be shaped by prenatal stressors.

Whether providing periodic exercise can reduce sow psychological stress through the temporary alleviation of confinement has not been previously studied. Earlier research primarily looked at the effects of periodic exercise on sow physical condition, evaluating such parameters as lameness score, sow postures, bone quality, reproductive performance, farrowing characteristics, umbilical blood flow, fetal growth and piglet mortality (Schenck et al., 2008; Harris et al., 2013).

The work within this literature review was conducted in response to the above-mentioned Code requirement. Unlike earlier reviews (McGlone et al., 2004; Rhodes et al., 2005; McGlone, 2013), which compare the influence of different housing systems on the welfare of gestating sows, this review is focused on evaluating whether the effects of periodic exercise on sow welfare could be evaluated through measurements of gestational stress, as determined by sow behaviour, health and stress physiology, the behavioural response of offspring to stress and sow reproductive performance and measurements of litter performance. These interactions will be explored through examination of the effects of gestational stress on the sow's reproductive physiology and comparing how the stress could be influenced in conditions that are known to cause stress and those that are known, or aim to reduce stress. Additionally, the motivational aspects of sow behaviour will be discussed in order to help evaluate the impact of confinement and periodic exercise to meet motivational needs and sow affective states. To support a thorough understanding, results from swine studies will be compared to those obtained from other species, housed in confinement. This work will evaluate whether the requirement of the Canadian Code of Practice for the Care and Handling of Pigs stating that "as of July 1, 2024, mated gilts and sows must be housed in groups, or in individual pens, or in stalls, if they are provided with the opportunity to turn around or exercise periodically, or other means that allow greater freedom of

movement,” (NFACC, 2014, pg.11) is appropriate and whether the implementation of this requirement would bring welfare benefits for the sows. It will also help to determine the directions for future research in the field of gestating sow welfare and reproduction and contribute to knowledge as to whether periodic exercise is a strategy to improve the welfare of stall-housed gestating sows.

2.2 Concerns over confinement of livestock

2.2.1 Factors influencing the welfare of confined farm animals

More than half of the world’s livestock are reared in intensive conditions (Hotzel, 2014). As society is becoming more aware of modern farming systems, public concern over animal husbandry methods is growing (Schau et al., 2013).

Factors that impact the welfare of confined animals include their physical (including the degree of physical restriction), and social environment, the animal-human relationship and the animal’s ability to control and predict events (Tennessen, 1989). Prolonged physical confinement may have deleterious consequences on the musculoskeletal system, making animals more predisposed to injuries due to decreased bone mineral content (Bell et al., 2001). Additionally, a continuous constraint on movement impacts behavioural responses leading to the development of abnormal behaviours due to an inability to perform species-specific motivated behaviours (behavioural deprivation). These behaviours with strong endogenous motivation include sleeping, eating, drinking, locomotion, copulation, grooming, social interaction and play behaviour (Sisto and Friend, 2001). For example, the removal of constraints on movement, such as release from a confined space, results in post inhibitory rebound locomotor behaviour (Sisto and Friend, 2001; Jones and McGreevy, 2007; Freire et al., 2009), with the amount of rebound locomotor activity increasing with the duration of confinement (Jensen, 2001). Jones and McGreevy (2007) identified that the complexity of the confined environment also affects the animals’ response to confinement: closely confined animals allot relatively less time to foraging or eating, in comparison to animals kept in an extensive naturalistic setting, which can result in unmet behavioural needs (not having an opportunity to express most normal patterns of functional behaviour that the animal is highly motivated to perform; Hughes and Duncan, 1988) and inactivity. For example, feed-restricted stall-housed sows after consuming their food ration are still hungry and highly motivated to forage, and so easily redirect their feeding motivation to

the trough or stall bars, showing oral stereotypies as a result of their unmet behavioural need and lack of satiety (de Leeuw et al., 2008). The performance of oral stereotypies can be reduced by providing roughage or other types of manipulable enrichment to confined animals, which gives them opportunities to express foraging behaviour (Tuytens, 2005) and also increase their satiety (Brouns et al., 1994).

Housing in confinement not only restricts the animal's movement but also results in alteration of social interaction patterns. For example, previous research has shown that stall-housed sows experience difficulties with establishing a stable hierarchy between animals in adjacent stalls and have a reduced number of social interactions in comparison to group-housed sows (Jensen, 1984). Additionally, stall-housed sows have been observed to experience an inability to resolve agonistic encounters with neighbours up to three times more often than it was observed between pen mates housed in groups (Broom et al., 1995). The restriction of sows to a stall and confinement next to their neighbour leads to the inability for them to resolve social conflict issues, triggering behavioural and physiological changes that indicate the animals find it stressful (Proudfoot and Habing, 2015).

To sum up, there are several clear restrictions from confinement, such as limiting the animal's ability to move and social pattern alterations, which can be stressful (Kirkden and Pajor, 2006a). Such stressful factors imposed on a pregnant female could have particularly detrimental effects because they affect not only the dam but also her subsequent offspring. This phenomenon is known as gestational, or prenatal stress (PNS), and has been shown to occur in a variety of animal species and humans (Lay et al., 2008; Patin et al., 2002), but to date the role of housing in the gestation stall on PNS has not been explored.

2.2.2 Sources of stress in gestating sows and their impact on sow welfare

Stress can be defined as a combination of the stimulus that disrupts the physiological balance of the organism, known as a stressor, and the behavioural and physiological reaction emitted by the organism to reestablish this balance, called a stress-response (Bartolomucci, 2007). Female pigs in intensive husbandry systems are exposed to both environmental and management-related stressors throughout their lives (von Borell et al., 2007). For example, they often face transportation, moving to a new environment, spatial restriction, social instability as a result of grouping with unfamiliar animals, feed restrictions, and, depending on the feeding

system and quality of management, a daily need to compete for resources, such as access to feed or lying space. Lack of good attitudes and handling by stockpeople can also be a significant source of stress in animals reared on intensive farms (Jones and McGreevy, 2007). Sexual behaviours are also restricted with sows most commonly restrained in stalls during estrus, as in most commercial barns artificial insemination is solely used for reproduction, and heat detection can be performed in the absence of a male animal; these behavioural restrictions may lead to stress and reduced sow welfare (von Borell et al., 2007).

In gestating sows, the combination and timing of stressors experienced is mostly dependent on the type of housing system utilized. There are plenty of gestating sow housing systems, in which sows are kept either individually (in stalls of different designs or individual pens) or in groups. Group housing systems differ in the feeding method (competitive or non-competitive feeding systems; some of the popular feeding systems are electronic sow feeders (ESF), floor feeding, shoulder stalls and free-access stalls), flooring, space allowance and the number of animals in the group (Kirkden and Pajor, 2006a). There are advantages and disadvantages to each gestation housing system design and, how the housing and management system can influence the sow should be considered when assessing sow welfare during gestation. Group gestation housing is promoted to enhance sow welfare through providing the sow with freedom of movement, societal interaction and an opportunity to make choices in her environment. However, sows housed in group settings face stressors, such as aggression from pen mates during mixing of unfamiliar animals at group formation, and competition for resources whether that be lying space, or gaining access to feed. The amount of stress experienced by group-housed sows over the course of pregnancy mostly depends on the kind of group housing system, with the type of a feeding system being a key factor, impacting the intensity and frequency of stress. For example, a floor feeding system allows all of the sows to eat simultaneously, which imitates their natural synchronized feeding behaviour (Verdon et al., 2015). However, this type of feed distribution triggers competition which can lead to aggression between sows at each feeding, which may lead to sows experiencing social stress on a daily basis. Moreover, such competition may cause variation in feed intake and, accordingly, undernutrition and low body condition in subordinate sows (Edwards, 1992). Feeding via an ESF allows for the greatest control over individual feed intake in comparison to other feeding systems (Verdon et al., 2015). But this system does not prevent aggression, as it forces sows to eat sequentially (Bench et al., 2013), and

animals may still compete to gain access to the ESF feeder. As sows are feed restricted, often there can be intense aggression around the ESF feeder as the sows queue up to get their feed once the 24-hour feeding cycle begins (Spooler et al., 2009).

Another variable that needs to be considered when evaluating the levels of stress and welfare of group-housed sows is the size of the group. However, it is often difficult to correctly assess the impact of this factor, as in most studies it is confounded with type of feeding system (Bench et al., 2013). For instance, Broom et al. (1995) found that sows, housed in small groups (five animals per pen) performed more oral stereotypies than the animals housed in a large group (38 sows per pen). The authors explain it as a consequence of the difference in pen sizes, but it is also important to take into account the difference in feeding systems used for this experiment (feeding stalls in small groups vs ESF in a large group). In the study of Broom et al. (1995) an actual space allowance differed only slightly (2.2 m² per sow in small groups vs 2.38 m² per sow in a large group). This study also showed that sows in large groups had more agonistic interactions upon initial mixing, but fought less throughout the first gestation, in comparison to those housed in small groups, which indicates that group size can change the social dynamics. Another source of social stress in group-housed sows is mixing them with unfamiliar sows (Otten et al., 2015), as it triggers aggressive encounters between the sows which are trying to establish a social hierarchy. In large dynamic groups this results in more injuries in newly added sows in comparison to sows which were introduced to the pen earlier (Bench et al., 2013).

In contrast to group-housing, stall-housing in gestation helps to provide all the sows with individual portions of feed, prevents sows from injuring each other during aggressive encounters and reduces aggression in general, as animals in stalls have limited social contact with other sows. However, the stall-housing system does not necessarily provide a higher level of sow welfare, as sows housed in stalls also experience multiple stressors, such as severe restriction of movement, inability to perform natural behaviours and having lack of control over the environment, altered social contact and, similarly to group-housing, significant food restriction.

Specifically, sows housed in gestational stalls experience severe space restrictions, preventing them from being able to walk or turn around. If the sow is large, standing up or lying down may also become difficult for her (Marchant-Forde, 2010). Prolonged inactivity caused by stall-housing may lead to reduced muscle tone and mass, bone strength, and an increased risk of lameness, which contributes to decreasing sow longevity (Schenck et al., 2008). Moreover,

restriction within a gestation stall is commonly accompanied by a lack of environmental enrichment or any other stimulation for animals (von Borell et al., 2007; Couret et al., 2009; Elmore et al., 2012), which severely limits the sow's behavioural repertoire and may increase the incidence of stereotypies (Marchant-Forde, 2010). On the other hand, individual housing reduces the number of aggressive encounters with conspecifics in contrast to group housing systems, where fighting can be regularly observed during feeding, and also after mixing (Jansen et al., 2007). But, at the same time, such social restrictions and an inability to resolve agonistic encounters with neighbours or move away from them can also become a significant source of social stress for stall-housed sows (Broom et al., 1995). When speaking about feed restrictions, a stall housing system seems to be advantageous, because it ensures the sow gets her daily feed allowance. However, it is important to understand that the commercial diets are limit-fed, so the sows remain hungry in both stall- and group-housing systems. Hunger enhances sow foraging motivation, which cannot be fulfilled in stalls due to the lack of complexity in the stall environment (Rhodes et al., 2005). It is also considered that the lack of control the sow has over her environment in the stall can adversely impact her welfare: she cannot separate lying and defecation areas, as well as adjust her location in according with an ambient temperature (Stolba and Wood-Gush, 1989), as she would do in a group situation. At the same time, the research of Rioja-Lang et al. (2013) on space utilization in pens with free-access stalls demonstrated that when having a choice to stay inside the stall or in the common group area, sows spent less than 5% of their time budget in the group area, with the parity 2-4 sows and heavier sows using group area more than younger and lighter animals. These results suggest that the levels of welfare in different housing systems can vary depending on individual sow characteristics: for example, in the study of Rioja-Lang et al. (2013) larger sows possibly preferred common group area because stalls restricted their movement and reduced levels of comfort to a greater extent than in smaller sows. At the same time, younger and lighter sows could prefer to stay inside the stalls, as stalls provided them with protection from aggressive encounters with dominant sows, and group area could not offer this protection.

The impact of the housing system on the welfare of gestating sows is covered in a review written by McGlone (2013). In terms of behaviour, the author reported a tendency for an increase in stereotypies in stalled sows in comparison to group-housed sows, following a review of seven years of research on housing systems (from 2005 to 2012). McGlone (2013) explained it as an

apparent change in sow genetics, since the basic housing systems have not changed. However, it is widely considered that feed restriction and the inability to express foraging motivation leads to the development of stereotypies (Verdon et al., 2015), so the above-mentioned conclusions are arguable because approaches to sow nutrition are also changing over time. On the other hand, changes in sow genetics could also make the sows more hungry, and hence both of these factors could contribute to an increase in stereotypies in stall-housed sows. Whilst some studies revealed a higher agonistic behaviour in group-penned sows (Jansen et al., 2007), others have indicated no significant difference in aggressive behaviour between groups and stall-housed sows (Hulbert and McGlone, 2006). Largely, the amount of agonistic behaviour experienced by sows in groups is dependent on the management of the system. On the whole, McGlone (2013) concluded that current scientific evidence for behavioural differences in pregnant sows kept in different housing systems is rather inconclusive because depending on the interpretation and emphasis placed on certain behaviours, it could be argued that one system is better than the other.

Determining the impact of the type of stress experienced in different housing systems is also important, due to the different physiological outcomes of acute and chronic stress responses. Exposure to acute stressors may be beneficial for both maternal and neonatal organisms. For example, Couret et al. (2009) demonstrated that piglets, delivered by gilts exposed to mixing on days 79-103 of gestation, had higher lymphocyte proliferation (enhanced immune function) in comparison to piglets born from gilts which were housed in stable groups throughout gestation. In contrast, the chronic stress response can be highly maladaptive: for instance, Yang et al. (2006) demonstrated that offspring from rats chronically stressed in the second and third trimesters of pregnancy had altered synaptic plasticity in the hippocampus, which could be related to impaired spatial learning and memory in prenatally stressed young rats.

Barnett et al. (1991) reported a significant elevation in basal free cortisol on days 30 and 57 of gestation in stall-housed gestating sows in comparison to group-housed sows, which supports the evidence that sows in stalls may exhibit a chronic stress response. In contrast, group-housed pregnant sows are usually exposed to a series of acute stressors, for example, those that follow mixing. The stage of the reproductive cycle at which the stressor (e.g. mixing) is applied may also affect the intensity of stress response and its consequences. For example, Stevens et al. (2015) showed that sows mixed one week after breeding had greater cortisol levels and performed aggressive behaviour more frequently than sows mixed at five or six weeks after

insemination. Such discrepancy can be explained by changes in hormone levels throughout gestation (Verdon et al., 2015). Interestingly, these behavioural and hormonal changes were observed only during the first week after mixing, which suggests that mixing is an acute stressor, considering that post-mixing aggression is reported to reach the peak at two hours post mixing, and then it significantly declines within 1-2 days after sow hierarchy is established (Stevens et al., 2015). Sows housed in dynamic groups show a higher frequency of acute stress response which follows their periodic mixing, as indicated by increased cortisol levels following every mixing in the study of Anil et al. (2006), in comparison to animals that are housed in static groups and mixed only once per reproductive cycle.

2.3 Assessing animal welfare

2.3.1 Animal welfare definitions and components

Animal welfare science is a mandated science, which means that it was developed for a particular social purpose and is used for the purpose of making policy (Fraser, 2008; Salter, 1988). In the case of animal welfare science, it emerged in the 1960s in response to ethical concerns regarding the well-being of animals housed in intensive farming conditions. The importance of animal welfare was acknowledged at the governmental level in the report of the Brambell Committee, which was appointed by the British government to investigate the welfare of animals kept in intensive housing systems (Thorpe, 1965). The Brambell Report (1965) defined animal welfare as a broad term, encompassing both the mental and physical well-being of the animal, which can be assessed through the evaluation of animal feelings, as determined by their physical structure, functioning and behaviour. Later, Hughes (1976, cited in Carenzi and Verga, 2009) also broadly defined animal welfare as “a state of complete mental and physical health, where the animal is in harmony with its environment,” (Carenzi and Verga, 2009, pg. 25). Finally, Broom (1986, pg. 524) defined welfare of an animal as “its state as regards its attempts to cope with its environment,” and considered it to be an individual characteristic of the animal rather than something given to it externally, and that animal welfare can be not only positive but also negative (Broom, 1991).

Since the time of publishing the Brambell Report, multiple scientists proposed concepts and definitions of animal welfare, which addressed different public concerns and were sometimes overlapping. One of the most commonly accepted approaches is the concept of the Five

Freedoms, which defines an ideal state of welfare and forms a framework for the analysis of animal welfare in different species and conditions (FAWC, 1993). These Five Freedoms include freedom from thirst, hunger and malnutrition; freedom from discomfort; freedom from pain, injury and disease; freedom to express normal behaviour and freedom from fear and distress (Webster, 2001).

Despite the Five Freedoms concept being widely recognized and influential among animal welfare scientists, modern thinking started to move towards ‘a life worth living’ concept, which suggests that merely freeing animals from survival-critical negative affects is not sufficient for good animal welfare, and that greater opportunities to experience positive affective states need to be given in order to provide a positive quality of life (Mellor, 2016). This idea is supported by current public views of modern farming: a survey on the US citizens’ views of an ideal pig farm conducted in 2015, showed that consumers considered pigs to be intelligent animals which deserve to have a happy life (Sato et al., 2017). Rather than focusing on freedom from the discomfort of being trapped in close confinement, 44% of the responders of this survey mentioned the concern about confined systems in general, stating that pigs need to be given plenty of space to roam, preferably having access to an outdoor area. Similarly, simply freedom from hunger was not an indicator of an ideal pig farm for the survey responders, with 36% of the participants stating that pigs need to be “well-fed” (Sato et al., 2017, pg.5).

Generally, three main components that must be considered when evaluating animal welfare which incorporate the Five Freedoms principles, and also involve measuring positive affective states in order to provide a life worth living, include: basic health and functioning, animal affective states and an ability to carry out ‘natural’ species-specific living (Fraser, 2008; Mellor, 2016). While measuring basic health and functioning through a variety of physical and physiological parameters is relatively straightforward, evaluating animals’ affective states is more challenging; affective states have a subjective component (Paul et al., 2020), which cannot be assessed directly. Measuring animal physiological responses, which sometimes overlap with basic health and functioning measures, as well as behavioural responses (spontaneous or learned) and mood assessment are the general categories of methods for the assessment of affective states (Ede et al., 2019). The natural living concept includes such parameters as an animal’s ability to perform natural behaviour, access to feed adapted to the animal’s physiology and living in the ‘natural’ environment (Lund, 2006). While assessing basic health and functioning as well as

affective states involves primarily animal-based measures of welfare, evaluating the natural living component also requires assessing animal housing and farm management strategies (resource-based and management-based measures; Munoz et al., 2018). However, often changes in the level of naturalness of animals' living environment are reflected in their basic health and functioning and affective states, which therefore can be used to evaluate the natural living aspect (Fraser, 2008; Mellor, 2016).

Due to this relationship, the current review will focus on animal-based measures, broadly divided into two categories of basic health and functioning assessment (including reproductive performance), and assessment of behaviour. Since the main topic of this review is the welfare of stall-housed gestating sows, the information on the methods of assessing animal welfare will be discussed in the context of evaluating pig welfare.

2.3.2 Stress: physiological, behavioural and evolutionary background

2.3.2.1 Physiological mechanisms of stress

According to current thinking, when challenged by a stressor, the body reacts using two main systems: hypothalamus-pituitary-adrenocortical (HPA) axis, and the sympathetic nervous system (SNS), that are working cohesively, generating two waves of the neuroendocrine stress response (Sapolsky et al., 2000). The first wave occurs within seconds of triggering the stress response by a stressor and includes an increased secretion of norepinephrine and epinephrine from the SNS, pituitary secretion of prolactin, pancreatic secretion of glucagon, release of corticotropin-releasing hormone by hypothalamus into the blood, and decreased secretion of gonadotropin-releasing hormone by hypothalamus, which is followed by decreased release of pituitary gonadotropins. The second wave follows the first wave and occurs within minutes. It involves the stimulation of adrenal glucocorticoid secretion by the HPA axis into the blood. Additionally, the SNS utilizes the sympathetic nerve endings that innervate every organ of the body to make the necessary physiological changes to cope with the stress challenge (Bartolomucci, 2007). Both systems have a downstream effect on other regulatory processes, triggering metabolic, cardiovascular and immune changes (Proudfoot and Habing, 2015), including increased cardiovascular tone which enhances substrate delivery to muscle, energy mobilization, immune activation as well as inhibition of reproductive physiology and behaviour (Sapolsky et al., 2000). Bartolomucci (2007) emphasizes that such a response is adaptive in the

short-term, but can be highly maladaptive in the long term. For example, long-term stress may depress immune function by altering the Type 1-Type 2 cytokine balance and suppressing numbers and function of immunoprotective cells (Dhabhar, 2014).

2.3.2.2 Gestational stress mechanisms

Stress experienced by gestating dams has been shown to have wide-ranging effects on the offspring's health and wellbeing (Rutherford et al., 2014). Gestational stress might affect fetuses in several ways. As shown in multiple species, including pigs, maternal glucocorticoids can be transported across the placenta, and affect the maturation of the fetal HPA axis, but the mechanisms of this influence remain unclear (Jarvis et al., 2006). Otten et al. (2015) analyzed the results of the studies, which included assessment of fetal cortisol regulation, and concluded that PNS may also be mediated by an increase in fetal cortisol release. Maternal stress can alter blood flow through the uterine arteries to the developing embryo, as shown in humans and primates (Teixeira et al., 1999), which leads to a decreased transport of nutrients to the developing fetus. This contributes to low birth weight and later health problems in offspring, such as predisposition to coronary heart disease, reported in humans (Barker, 1997). An impaired blood flow in the uterine arteries can lead to the intrauterine growth retardation, as shown in humans (Frusca et al., 1997). Although the effects of gestational stress on uterine blood flow have not been confirmed in pigs (Harris et al., 2013), these effects are considered to affect sow reproductive performance and offspring development, and therefore this topic warrants further investigation. Another indirect effect of gestational stress on the developing fetus may lie in the alteration of placental functioning (Otten et al., 2015). An increase in maternal glucocorticoids can alter placental trophic or endocrine function by changes in transplacental glucose and iron transport to the fetus, as shown in rats and monkeys (Langdown and Sugden, 2001; Coe and Lubach, 2005), or lead to increased production of corticotropin-releasing hormone by the placenta in primates, which activates the fetal HPA axis (Merlot et al., 2008). However, despite being known, these effects have not yet been identified in pigs.

2.3.2.3 Physiological and behavioural outcomes of gestational stress for offspring

Prenatal stress effects depend on the stage of gestation when an organism is exposed to stress: in early pregnancy, it is associated with pregnancy loss, whereas in mid- and late gestation

it can result in reduced birth weight and impaired growth, lower immunity, altered neuroendocrine activity and behaviour (Brajon et al., 2017). For example, stress experienced by the dam in mid-to-late gestation has been found to lead to altered social behaviour and an increase in anxiety-like behaviours to challenging situations in pigs (Jarvis et al., 2006; Merlot et al., 2008; Couret et al., 2009; Otten et al., 2015). Apart from that, intensity, duration and type of stressor also greatly affect the outcomes of gestational stress.

In humans, PNS can lead to preterm deliveries (work-related chronic stress; Homer et al., 1990) and altered developmental outcomes for the offspring: lower performance of motor development and cognitive abilities (as a result of PNS, induced by a short-term natural disaster), and long-term behavioural abnormalities, such as aggressiveness and destructiveness (due to long-term perceived pregnancy-related stress; Mulder et al., 2002; King et al., 2012). Rodent studies have also revealed that when the mother is periodically stressed (restraint stress or repeated resident intruder confrontation procedure for pregnant females) throughout or in late gestation only, the progeny have a significantly lower average birth weight, which may be associated with health problems in later life (Henry et al., 1994; Gotz et al., 2008). The lower birth weight can be a result of increased uterine artery resistance index in stressed gestating females (Teixeira et al., 1999). Interestingly, chronic maternal anxiety can also affect fetal behaviour, as demonstrated in ultrasound studies (Ianniruberto and Tajani, 1981; Groome et al., 1995).

Gestational stress may also lead to some immunological alterations: for example, psychosocial stress (repeated resident intruder confrontation procedure for female rats, which is based on the defence of a home cage by a resident experimental female from unfamiliar females transferred to the same cage) applied daily for two hours throughout pregnancy, decreased blood lymphocyte numbers and lymphocyte proliferation (Gotz and Stefanski, 2007a; Gotz and Stefanski, 2007b). However, repeated social stress in the pig (repeat social mixing twice a week over a period of four weeks in early (days 24-48) or late (days 79-103) gestation), did not impact blood lymphocyte numbers in offspring. Furthermore, piglets from gilts experiencing social stress (mixing) between days 79 and 103 of gestation, had a higher lymphocyte proliferation in comparison to those not stressed prenatally (Couret et al. 2009). In contrast, Tuchscherer et al. (2002) found, that restraining sows with five minutes of daily restraint stress (restraint with a nose sling) in the last five gestational weeks resulted in decreased serum immunoglobulin G

(IgG) concentrations, decreased lymphocyte proliferation in suckling piglets, whereas natural killer cell cytotoxicity was not changed. Moreover, morbidity and mortality during the suckling period in these animals were higher than in control litters, which may be related to the decreased permeability of the neonatal small intestine to antibodies due to being prenatally stressed, as IgG concentration in colostrum of stressed and control sows in this study did not differ. This discrepancy of results in the two above-mentioned studies may be explained by the nature of treatment applied to the sows, as mixing with unfamiliar animals, used in the study of Couret et al. (2009) induced more moderate stress which can be experienced in the natural environment, whereas in the experiment conducted by Tuchscherer et al. (2002) it was rather a repeated acute unnatural stress. These results suggest that PNS has a significant negative impact on the immunity in offspring of different species, and the immune system of prenatal piglets can be particularly affected by chronic gestational stress in their mothers.

It is important to understand, that results obtained from the PNS studies are not necessarily relevant across species. Rodent data cannot be extrapolated to other mammal species, due to their different evolutionary background: the maturation of the rodent brain reaches the highest point much later in pregnancy in comparison to more precocial species, including most ungulates (Baxter et al., 2016). Moreover, the gestation length, prenatal developmental timeline (and, consequently, period of pregnancy when the stressor is applied, as well as the duration of its application), and also placenta's permeability to hormones differ between species (Couret et al., 2009). Additionally, the types of stressors also greatly vary across species (for example, due to different rearing conditions). Therefore, species-specific studies need to be conducted.

Relatively less information is available on the effects of PNS in farm animals, but results of the studies conducted in farm species also indicate its presence and impact on the pregnant dam and neonates. For example, the offspring of female goats penned at increased stocking densities (3.0 m² vs 1.0 m² per animal – for the control vs high animal density treatments) throughout gestation showed a greater fearfulness compared to controls, i.e. performed more escape attempts in a separation test, and vocalized more in social and separation tests (Chojnacki et al., 2014). Similar outcomes were obtained in sheep (Averos et al., 2015), showing higher emotional reactivity and fear response during a novel arena, a novel object, and a social motivation tests in lambs from mothers, exposed to decreased space allowance during gestation in comparison to those housed in medium and low densities (1.0 m² vs 2.0 m² and 3.0 m² per ewe, accordingly).

Baxter et al. (2016) showed that aversive handling of goats during mid gestation led to poorer placental quality (fewer number and smaller size of cotyledons), whereas gentle handling had a positive effect on maternal behaviour, and particularly on maternal attentiveness (more time spent in grooming and nosing behaviour). Such focused attention stimulates suckling by the offspring and thus promotes its survival. In swine research, piglets that were prenatally stressed by social mixing stress applied on days 39-45 and 59-65 of pregnancy to their mothers, showed behavioural inhibition, expressed as the increased time of lying behaviour, reduced exploration, locomotion play, fighting play and mounting behaviour in comparison to non-stressed piglets, starting six days after weaning (Brajon et al., 2017). According to the authors, these effects may be the signs of depressive-like behaviour. Kranendonk et al. (2006) simulated prenatal stress in three groups of gestating sows by oral administration of hydrocortisone acetate in early, mid or late gestation, and found that piglets from all prenatally stressed treatments during mixing at 48 days of age had more aggressive and fewer non-aggressive encounters and spent less time in social interactions in the home pen at day 14 of age, than not prenatally stressed piglets. Additionally, piglets from the sows which were administered hydrocortisone acetate in early and late gestation had higher locomotion and vocalization levels during the novel environment test. These results suggest that the PNS experienced by a sow can negatively alter the behaviour of her piglets, as they become more anxious (according to the new environment test results) and less prepared for social confrontations in the future, as indicated by the results of the mixing test which showed that prenatally stressed piglets had reduced abilities to resolve social conflicts without aggression (Kranendonk et al., 2006). These behavioural changes may contribute to elevated levels of social stress due to altered social behaviour later in life, and hence poorer welfare.

2.3.3 Basic health and functioning assessment

In pig welfare studies, the basic health and functioning component of animal welfare assessment involves a range of measures, which include such physiological parameters as body temperature, heart and respiratory rates, levels of stress hormones (cortisol, adrenocorticotrophic hormone (ACTH), dehydroepiandrosterone), immunological response (neutrophil:lymphocyte ratio, natural killer (NK) cell activity); physical parameters, such as presence and severity of injuries and lameness; and also sow reproductive performance and piglet physiology (weaning-

to-estrus interval, farrowing rate, farrowing duration and farrowing interval, standard productivity measures, piglet size at birth, preweaning mortality, placental morphology). This variety of measures provides information on specific physiological functions that can be used to evaluate welfare.

2.3.3.1 Physiological measures

Physiological measures have been extensively used to evaluate swine welfare. For example, Ruis et al. (2001) used changes in body temperature to assess a hypothermic reaction to stressors. The authors measured body temperature in low (those that made fewer escape attempts in a backtest performed at 2-4 days of age) and high (those that had more escape attempts during the backtest) behaviorally resistant prepubertal gilts before and after placing them in social isolation. It was found that in both groups body temperature decreased significantly in response to isolation. Additionally, in high resistant gilts body temperature did not recover during three weeks of isolation, but in low resistant gilts body temperature returned to normal within one day. This observed hypothermic reaction to the stressor is possibly related to the central activity of a naturally occurring antipyretic vasopressin (Chen and Hebert, 1995; Yang and Gordon, 2002). Marchant et al. (1997) reported that gestating sows housed in stalls had higher basal heart rate and average heart rate during feeding than sows housed in small or large groups, which could be explained by a greater sympathetic nervous response induced by long-term confinement or by reduced cardiovascular fitness in stall-housed sows. Increased respiratory rate of growing pigs was shown to be related to acute and chronic heat stress, which can be explained by the stimulation of the hypothalamus due to increased body temperature, resulting in sending an impulse to the respiratory system in an attempt to eliminate heat by evaporation through an increased respiration rate (de Oliveira et al., 2018).

These examples demonstrate that changes in physiological measures can be a good indicator of stress experienced by pigs housed in intensive conditions, and information obtained from taking these measures needs to be taken into account when evaluating pig welfare.

2.3.3.2 Immunological measures

Assessing immunological changes has also been used as an attempt to evaluate swine welfare and in particular to assess both acute and chronic stress. Salak-Johnson et al. (1997)

showed that administration of porcine corticotropin-releasing hormone (and simulating an acute stress response) resulted in lower NK cytotoxicity at 1 h post injection and higher neutrophil:lymphocyte ratio at 1 h and 2 h after injection in comparison to control pigs receiving a saline injection. The changes in NK cell activity have been previously demonstrated to be correlated with the changes in the levels of catecholamines indicating the presence of acute stress (Schedlowski et al., 1993), presumably due to direct interaction of catecholamines with NK cells through β -adrenergic receptors on NK cells. Karlen et al. (2007) found that stall-housed sows had a higher neutrophil:lymphocyte ratio at 15 weeks of pregnancy in comparison to the sows housed in large groups on deep litter, which could indicate the presence of chronic stress in the stall-housed animals, accumulated over gestation. The prolonged increase in glucocorticoid levels during chronic stress has been previously reported to cause neutrophilia and concurrent lymphopenia in mice through the glucocorticoid-inducible protein lipocortin 1, which down-regulates leukocyte function (Harris, 1995; Hickman, 2017). At the same time, Hulbert and McGlone (2006) did not find differences in neutrophil:lymphocyte ratios between stall-housed and group-housed sows with the trickle-feeding or drop-feeding system at mid gestation. However, the authors of the latter study did not take immunological measures in advanced pregnancy. These results suggest that the levels of chronic stress experienced by sows at mid gestation were not high enough to cause immunological changes; however, by the end of gestation chronic stress became stronger and was able to impair sow immune function, as demonstrated by the study of Karlen et al. (2007).

The findings of the above-mentioned studies suggest that immunological measures can reflect the presence of stress that could lead to reduced welfare levels; however, using the neutrophil:lymphocyte ratio as a measure of chronic stress in swine needs to be further explored. The studies of Hulbert and McGlone (2006) and Karlen et al. (2007) indicate that this measure may not be sensitive enough to detect milder levels of chronic stress, based on the assumption that stall-housed sows accumulate chronic stress over the course of gestation. Other possible explanations include an assumption that chronic stress in stalls may not be severe enough to cause changes in sow immune function, or that sows habituate to the living environment in stalls and hence their levels of stress lower as gestation progresses.

2.3.3.3 Physical measures

Evaluation of the presence and severity of body lesions and locomotor problems, such as lameness, is a cheap, quick and effective method of assessing pig welfare which is widely used. These measures indicate the presence of animal interactions that could be stressful (i.e. body lesions from aggression) and painful health conditions (i.e. lameness). Physical measures can help to identify problems with housing, feeding system or management practices (for example, higher incidence of lameness in sow group pens with inappropriate flooring or increased lesion scores due to aggression in group pens with competitive feeding systems), which contribute to poor welfare. For instance, Bos et al. (2016) compared lameness scores and skin lesion prevalence between static and dynamic groups of gestating sows and found that sows housed in static groups had lower skin lesion prevalence and lameness scores at the end of gestation in comparison to the sows from dynamic groups. The higher lesions and lameness observed in dynamic groups were believed to be linked to increased levels of aggression and fighting in repeatedly mixed animals due to establishing a social hierarchy. Given the specifics of the dynamic group housing management type, it can be implied that these results represent the effects of repeated short-term acute stress responses, which potentially could escalate into chronic stress. In another study, Salak-Johnson et al. (2007) reported that gestating sows housed in group pens with a space allowance of 1.4 m²/sow had higher shoulder and rear lesion scores (recorded daily during days 25-38 of gestation and weekly from day 38 until farrowing) in comparison to the sows housed in the groups of the same size, but with space allowances of 2.3 m²/sow or 3.3 m²/sow. Additionally, sows housed in pens with the lowest space allowance had the lowest BCS, and sows housed in groups with the highest space allowance had the largest litter size. Based on this evidence it can be assumed that the sows which were housed in the smallest pens experienced more chronic stress during gestation, which was represented not only by reduced reproductive performance and poorer feed conversion but also by increased lesion scores. Turner et al. (2006) studied the relationship between localization and severity of lesions and aggression in group-housed growing pigs. The authors found that both pigs involved in reciprocal fighting and those being bullied had higher lesion scores in comparison to pigs which avoided fighting and receipt of bullying, suggesting that pigs with higher lesion scores had poorer welfare not only due to experiencing pain caused by lesions but also due to the experienced social stress. The authors also concluded that pigs engaging mostly in reciprocal fighting had the greatest proportion of lesions around the front third of their bodies, while those

being bullied had a higher proportion of lesions around the rump area due to biting. In another study, Turner et al. (2017) explored how regrouping behaviour influences lesions at 24 h, as an indicator of acute stress, and at three weeks post regrouping, as an indicator of chronic stress. The authors found that pigs receiving the lowest number of lesions to the front of the body at regrouping and three weeks after regrouping behaved as ‘unaggressive losers’ and ‘aggression avoiders’. Similarly, pigs receiving the lowest number of lesions to the whole of the body at regrouping and three weeks after regrouping behaved as ‘aggression avoiders’. In contrast, pigs that had the highest number of lesions to the front of the body and the whole of the body at both data collections were classified as ‘extreme aggressors’. Interestingly, over the course of three weeks after mixing lesion scores went down, but a substantial number of lesions was still observed. At three weeks post regrouping the highest observed number of lesions to the front of the body was 63, and the highest total lesion count on the body was 115 (in comparison to 99 and 199 lesions recorded at regrouping, accordingly). These findings indicate that aggression in group pens is present not only at regrouping, but also in stable social groups, and lesion scores can indicate the presence of both acute and chronic stress, with aggressive pigs having the highest lesion scores.

The above-mentioned studies demonstrated that evaluation of physical parameters can be successfully used to assess pig welfare. However, this approach has some limitations. For example, lameness scoring is a subjective method, the results of which can significantly differ across observers. Pfeifer et al. (2019) calculated inter-observer and intra-observer reliability coefficients for three observers during on-farm self-assessment of animal welfare and found that the inter-observer reliability for lameness scores was poor (intra-class correlation coefficient = 0.36). This means that the choice of methods used to assess physical parameters of welfare needs to be critically evaluated; in the case of lameness, for example, it has been proposed that automated detection may improve the reliability of results in comparison to traditional gait scoring method (Pedersen-Macnab et al., 2020).

2.3.3.4 Hormonal measures

Another approach to evaluating pig welfare involves assessing the levels of stress-related hormones, with cortisol being the most well studied and widely used indicator of stress (Heimborge et al., 2019). The increase in cortisol production by the cortex of the adrenal gland

happens as a part of a stress-response of the HPA axis, and it is preceded by the release of corticotrophin-releasing hormone by the hypothalamus, which stimulates the anterior pituitary gland to release adrenocorticotrophic hormone into the blood (Fraser, 2008). While physiological mechanisms of acute and chronic stress are similar and both involve the HPA axis activation, these two types of stress are differentiated based on the duration and frequency of the stressor, with exposure to chronic stress (continuous stress or a series of acute stressors) leading to pre-pathological states and possibly to a pathological condition (Moberg, 2000). Serum and salivary cortisol as a measure of acute stress, and to a lower extent urinary and faecal cortisol concentrations as a measure of chronic stress have been previously measured in an attempt to evaluate the activity of the HPA axis (Meyer and Novak, 2012; Casal et al., 2017). In pig studies, for example, Ison et al. (2010) demonstrated that gestating gilts had higher salivary cortisol levels in the days following mixing with unfamiliar animals, in comparison to their salivary cortisol concentration on the day before mixing, which confirmed the hypothesis that mixing is a stressful event. However, using of the above-mentioned methods has several limitations, as they can provide information about the activity of the HPA axis within the short (from a few minutes to one or two days) period of time, and hence are most effective when trying to measure acute stress (Heimburge et al., 2019). Additionally, the values of these measures are influenced by circadian rhythms and can be affected by environmental disturbances (Meyer and Novak, 2012) and stressful sampling approaches, including handling during collection of salivary and blood samples and an invasive blood sampling procedure. For instance, Karlen et al. (2007) did not find significant differences in salivary cortisol concentrations in gestating sows housed in stalls or large groups on deep litter on weeks one and nine of gestation, even though other measures which help to evaluate welfare, such as the number of scratches, incidence of lameness, neutrophil:lymphocyte ratio, farrowing rate and the numbers of weaned piglets differed between the housing systems. These results suggest that the changes in salivary cortisol concentration in the current study did not reflect the presence of chronic stress: possibly salivary cortisol levels increased right after mixing in response to an acute stressor, but by day five when the salivary samples were collected, the cortisol levels dropped; however, this hypothesis was not tested in the study of Karlen et al. (2007). Overall, the results suggest that the salivary cortisol concentration was not an optimal method for measuring welfare in the current study.

The analysis of cortisol in hair is a relatively new measurement for swine research and it has been proposed as a chronic measure of the cortisol to evaluate stress over a longer period of time, which has previously been successfully used in other species and human research (Creutzinger et al., 2017; Trevisan et al., 2017; Heimbürge et al., 2019). This method works on the assumption that cortisol is incorporated into the hair as it grows. The mechanism by which cortisol is incorporated into the hair is not yet fully understood (Meyer and Novak, 2012). Based on forensic toxicology studies on incorporation of lipophilic drugs into the hair shaft, it is considered that the main mechanism of incorporation is the delivery of lipophilic substances (including cortisol) from the bloodstream to the hair follicular cells during the hair growth phase (Barroso et al., 2011). A secondary pathway of hair cortisol incorporation in pigs is considered to be a passive diffusion from surrounding tissues and sebum (Meyer and Novak, 2012; Casal et al., 2017). Additional mechanisms include local cortisol production by the hair follicle itself, which was discovered in humans (Heimbürge et al., 2019), and external contamination (Barroso et al., 2011). Measuring hair cortisol levels is a non-invasive technique, and it offers advantages such as the opportunity to obtain results from very small samples, the ability to store the samples at room temperature before analysis (Macbeth et al., 2010), and also an opportunity to evaluate the levels of stress during a certain period of time if the rate of hair growth is known. It has been previously reported by Bacci et al. (2014), that the mean rate of hair regrowth for sows is 0.7 ± 0.2 cm/month. To date, very few studies used this measure to evaluate pig welfare, but the initial results look promising. For example, Prims et al. (2019) demonstrated that artificially reared female piglets exposed to overcrowding and frequent mixing during the weeks 2-4 of life had significantly higher hair cortisol levels than the piglets not exposed to the above-mentioned stressor. At the same time, stressed piglets also had lower weight gain in comparison to control non-stressed piglets, confirming that they had reduced welfare levels. Interestingly, in this study salivary cortisol concentrations did not differ between treatments, providing evidence that hair cortisol represents chronic stress better than salivary cortisol. Morgan et al. (2019) showed that piglets which underwent surgical castration, teeth clipping and tail docking, and were housed without environmental enrichment, had higher levels of hair cortisol over the periods from birth to weaning and from weaning to slaughter, in comparison to piglets housed in an enriched environment, for which invasive procedures were avoided and immunological castration was performed. Roelofs et al. (2019) found no effect of parity on hair cortisol concentration in group-

housed gestating sows. Given that the hair samples collected in this study reflect the second and third trimester of gestation, the authors conclude that on-farm stressors encountered by sows during gestation remain stressful even if these stressors are familiar to the sows. The authors also reported a positive correlation between sow hair cortisol levels during the second and third trimesters and litter size, but whether this relationship represents a higher level of gestational stress experienced by sows carrying larger litters, or whether this is a physiological gestational effect in response to larger litters, needs to be further investigated. Everding et al. (2020) compared hair cortisol levels in stall-housed and group-housed gestating sows and found that parity 0-1 stall-housed sows had elevated levels of hair cortisol in comparison to parity 0-1 group-housed sows, with parity 2-3 and 4-6 sows from two housing systems being no different. These results suggest that while older sows experienced similar levels of stress in different housing systems, for young sows the levels of gestational stress differed depending on the housing system, assuming that hair cortisol levels in the study of Everding et al. (2020) reflected the levels of stress and not a physiological response to pregnancy.

To sum up, the initial studies measuring the levels of cortisol in swine hair demonstrate that it offers a promising method for animal welfare assessment, with hair cortisol analysis being a promising method for measuring chronic stress. This would be a particularly useful method to assess the levels of gestational stress in pregnant sows, as it allows an evaluation of overall levels of stress, from which to interpret sow welfare during a prolonged period of gestation.

2.3.3.5 Productivity measures

The analysis of productivity measures is an objective auxiliary method that can be used in conjunction with other methods to contribute to the evaluation of sow welfare. It is also inexpensive, given that the required labour is typically readily available in the barn and that productivity measures usually are already collected by the barn staff as they are of interest to understanding production. Curtis (1987) proposed that measuring productivity traits is one of the most reliable indicators of animal welfare on a farm level to assess herds. However, in modern farming, there are several factors that influence the correlation between the productivity levels and welfare, such as genetic selection for production traits at the cost of declining health and welfare in productive animals, and active targeted use of hormones and other interventions which increase productivity (Fraser, 2008). Nevertheless, evaluation of productivity can provide some

useful insight into the levels of sow welfare, as demonstrated in the study of Morgan et al. (2018). The authors found shorter mean weaning-to-weaning cycle length, overall farrowing rate and a tendency to have a higher number of total born and liveborn piglets in group-housed sows in groups of different sizes mixed at 28 days of gestation, in comparison to stall-housed sows. This increase in productivity could be observed due to the physiological changes that could have improved sow health, due to sows experiencing lower levels of stress in group settings. Additionally, injuries and a lameness index recorded every two weeks during gestation significantly improved in group-housed sows in this study, which suggests that group-housed sows had better welfare than stall-housed sows.

Some of the productivity measures can indicate the presence of acute stress: for example, acute stress experienced by pregnant sows which are mixed during the peri-implantation period can increase embryo mortality and hence result in reduced conception rate and litter size (Arey and Edwards, 1998). In contrast, other productivity measures can be related to chronic stress: for instance, sows experiencing chronic heat stress during gestation were demonstrated to have reduced duration of gestation and lower piglet birth weight (Lucy and Safranski, 2017).

The presented evidence suggests that productivity measures can be used as a part of pig welfare assessment and they potentially can help to indicate the presence of acute and chronic stress. However, these measures must be evaluated only in conjunction with other basic health and functioning and behavioural parameters.

2.3.4 Assessment of behaviour

Behavioural evaluation in pigs includes collection and analysis of measures such as performance of maintenance behaviours and stereotypies; learned behavioural responses (in preference and motivation tests) and mood assessment through cognitive bias tests.

2.3.4.1 Maintenance behaviours

Assessment of maintenance and stereotypic behaviours are more commonly used methods of evaluating pig welfare in comparison to the evaluation of learned behavioural responses and mood assessment, as they are limited to observations and do not require expensive equipment or any special training of animals. Fraser (1983) defined maintenance behaviours as mostly innate instinctive behaviours which are vital to the animals in their integration and mediation with their

environment, as opposed to abnormal behaviours, which arise when animals experience some behavioural deficits, primarily associated with housing in intensive systems. The author described 48 maintenance behaviours in pigs, grouped in such categories as reactivity (including reflex activities representing the first line of defense, agonistic activities and vocalizations), ingestion, exploration, movement, association (social behaviour), body care, territorialism and rest. The full list of maintenance behaviours is covered in the article of Fraser (1983). These behaviours also include specific behaviours that are exhibited in natural free-ranging conditions (Fraser, 1983), called natural behaviours. While evaluation of all of the maintenance behaviours can give an insight into the level of welfare, some of these behaviours have been studied in commercially raised pigs more often than other behaviours. For example, Anil et al. (2002) looked at postural behaviour in stall-housed sows of different sizes, and found that when the stall size was smaller relative to the sow size, the transition time between postures was longer than in smaller sows, for which the stall size was larger relative to the sow size. A negative correlation between the stall length relative to sow length, and the duration of time spent standing was also reported (Anil et al., 2002). The authors related these findings to a decreased level of comfort and hence lower welfare in relatively large stall-housed sows in comparison to smaller sows, housed in the stalls of the same size. In another study which looked at sow social behaviour as a welfare indicator, Remience et al. (2008) reported that an increase in space allowance from 2.25 m²/sow to 3.0 m²/sow in dynamic groups with ESF significantly decreased the performance of one-way aggressions in the days following mixing, which possibly resulted in a lower incidence of skin lesions. The findings of Remience et al. (2008) suggest that the evaluation of maintenance behaviours can provide useful information not only about an animal's mental state but also about its physical condition, as determined by skin lesion scores.

While being useful for evaluating the levels of gestating sow welfare in general, assessment of specific housing system-related maintenance behaviours is also important. For example, the evaluation of postural behaviour is useful for studying sow welfare in stalls, as demonstrated by the studies on the effects of providing rubber mats in feeding stalls (Calderon Diaz and Boyle, 2014) and on the effects of stall size (Li and Gonyou, 2007). Sitting (intermediate posture between standing and lying) has also been classed as an indicator of difficulty to change posture, for example in a narrow stall (Li and Gonyou, 2007). Aggression is an important indicator of the presence of acute and chronic stress and, hence, sow welfare, as competition for resources

(primarily food) and establishing social hierarchy are the main factors that trigger aggression (Maes et al., 2016) in different housing systems.

2.3.4.2 Stereotypies

Stereotypies can be defined as repetitive behaviours that lack variance and have no obvious function or goal (Mason, 1991). Stereotypies are derived from various source behaviours, which are originally normal behaviours that become abnormal when redirected from their typical target to some different and inappropriate target (Fraser, 2008). Depending on the source behaviour, stereotypies can be oral or locomotor, and in pigs oral stereotypies are prevalent. Wiepkema and Schouten (1992) described the process of developing stereotypies using the example of tethered sows: the sows were fixed with a tether while eating a small meal, and after finishing the meal the sows discovered that they were tethered and started to bite and pull the chain of the tether and push against the bars of the stall attempting to break out. With time, these behaviours became simpler and organized in repetitive constant sequences, which were particularly intensive around feeding time, suggesting that this activity to break out partly represented redirected foraging behaviour and that not only the restriction of movement but also hunger stimulated the development of stereotypies. The latter idea was confirmed by the study of Terlouw et al. (1991), who found that regardless of being housed in narrow stalls with tethers or in group pens with hanging chains, sows receiving food at restricted commercial levels performed more stereotypies than the sows fed twice the amount of the commercial rations. Performance of stereotypies is considered to be an indicator of poor animal welfare for several reasons: first, the disruptions in the functioning of the basal ganglia in the brain caused by the use of stimulating drugs or due to injuries were demonstrated to trigger the development of stereotypic behaviour in animals, suggesting that the conditions which lead to the development of stereotypies possibly negatively affect the brain functioning (Fraser, 2008). Secondly, it was demonstrated that the activation of HPA system is linked to the development of stereotypies: Salak-Johnson et al. (2004) reported that pigs which were injected with corticotrophin-releasing hormone into the brain ventricles responded with several behavioural reactions, one of which was the development of stereotypies. Lastly, the fact that the studies of Terlouw et al. (1991) and Wiepkema and Schouten (1992) demonstrated that such aversive (as determined by other measures of welfare) factors as hunger and housing in close confinement stimulated the development of stereotypies in sows, suggests

that the performance of stereotypies is a critical measure of pig welfare (McGlone, 2013). Therefore, this parameter has been used repeatedly to evaluate the welfare of gestating sows. For instance, Karlen et al. (2007) reported that stall-housed sows performed more bar and trough biting, licking and nosing in comparison to the sows housed in large groups on deep litter. This difference was significant at week one after breeding, and the strong tendency was still present at week nine post breeding. Based on these results, the authors concluded that stall-housed sows possibly experienced some welfare disadvantages in comparison to the group-housed sows. This could be due to the confinement stress experienced by stall-housed sows, due to the lack of the opportunities to perform innate behaviours, such as rooting, in the barren stall environment, and possibly because of higher levels of hunger in stall-housed sows, as even though the animals in both housing systems were receiving the same feed rations, sows housed on deep litter could consume bedding and feel more satiated than stall-housed sows. Similarly, in the study of Chapinal et al. (2010) stall-housed sows were observed performing stereotypies more frequently than group-housed sows, with the increase of performing stereotypies post feeding. The authors also reported that gilts performed stereotypies less frequently than adult sows in all housing systems. These findings are consistent with previously discussed studies and suggest that feed and space restrictions play a major role in the development of stereotypies. The presence of the parity effect also confirms the idea of the presence of the cumulative effect of confinement stress and feed restriction.

Based on the mechanisms of development, and also given that previous studies found differences in the levels of stereotypies in gestating sows, housed in the same housing systems for a prolonged period of time, it can be concluded that the evaluation of the stereotypy levels can provide information about the presence of chronic stress and reduced levels of welfare.

2.3.4.3 Learned behavioural responses

Similarities in human and animal neural anatomy, as well as physiological and behavioural responses to stimuli suggest that animals are capable of feelings, and most animal welfare scientists consider feelings to be an important component of animal welfare (Kirkden and Pajor, 2006b). However, as the direct observation of subjective experiences in animals is not possible, the indirect methods of assessing animal feelings were developed. One of the approaches to assess subjective animal feelings is through the evaluation of learned behavioural responses. This

approach is based on giving animals some control over their environment and observing the decisions and choices they make, which are shaped by the animal's awareness of the contingencies and of the test situation in general (Kirkden and Pajor, 2006b; Ede et al., 2019). The key difference between preference and motivation tests is that in preference tests animals have two or more alternate resources to choose from, and quantification of their motivation to obtain the preferred resource is not performed, whereas in motivation tests the animal's motivation to access the resource is quantified, and a different option of resource is not necessarily given (Kirkden and Pajor, 2006b). Evaluating the motivational strength is useful because it is thought that if the environment prevents the animal from performing a behaviour which it is strongly motivated to perform, then the animal will likely have poorer welfare (Dawkins, 1990). To evaluate the strength of motivation in motivation tests, a resource of known value needs to be used as a comparator. In one of the early studies, the strength of hens' motivation to access litter for dust bathing was studied through giving hens access to two cages, one of which contained litter, and another containing food (Dawkins, 1983). Changing the duration of food deprivation before testing, it was discovered that satiated birds were choosing the cage with litter more often, but the hens which were food-deprived for 12 h generally chose the cage with food. The hens which were deprived of food for 3 h chose food and litter equally, which led to the conclusion that the hens' motivation for litter is equal to their motivation to access food when they are mildly hungry. In the field of pig studies, Patterson-Kane et al. (2011) also demonstrated that food is a resource of known high value, and developed a food-metric scale, which provides a means to standardize and quantify the effort performed by pigs when offered different resources. One of the successful examples of the preference test use is the study of Tuytens et al. (2008), who studied lying comfort of gestating sows with regard to the type of bedding. The authors offered polyurethane-PVC mats to group-housed gestating sows in an open-choice test and found that the occupancy of lying areas with a mat was higher in comparison to the same and other lying areas (with solid concrete flooring) without the mat, which suggests that such enrichment can enhance sow lying comfort and hence improve sow welfare. As for the motivation tests, Elmore et al. (2012) used this approach to evaluate sow motivation to access compost and straw in comparison to food (based on the food-metric scale concept) and negative control (empty trough). The authors reported that sows showed higher operant responding (a measure of effort to access the resource) and lower latency to press the

operant panel for food and compost in comparison to the empty trough, and also higher resource use (higher percentage of time spent in interaction with the resource) for straw. Overall, this study demonstrated that sows value having access to environmental enrichment, as indicated by operant responding and resource use, and while the technique used for measuring motivation in this study allowed to quantify and compare sow motivation to access different resources, it also has several limitations. For example, for each sow the motivation was measured for only one resource, so the comparison of motivation for different resources within the same animal was not possible, and hence the results of the study may be influenced by sow individual preferences. Additionally, in the study of Elmore et al. (2012) an operant panel with a single button was used, which makes it difficult to confirm that the levels of interaction with the panel reflect the pure motivation of sows to access a certain resource, rather than motivation to explore the panel as a novel object and play with it. This experimental design would benefit from the use of a more complex model of the panel, for example it could contain two buttons, one resulting in receiving of a reward and one serving as a control measure; then the levels of interaction with the ‘rewarding’ button would show that the sow is aware of why she is interacting with this button.

Motivation studies can potentially help to detect the presence of chronic stress, symptoms of which are parallel to depression in humans, based on the fact that chronic stress was proven to impair motivation for reward, as demonstrated based on the study of the rat model (Kleen et al., 2006). In general, studies of learned behavioural responses can be of great use in animal welfare studies, as they help to objectively assess and quantify animal affective states and the underlying motivations for resources.

2.3.4.4 Mood assessment

Mood assessment, which directly considers the cognitive component of emotional processes, is a useful tool for evaluation of affective states in animal welfare studies (Paul et al., 2005). Cognitive approaches provide an approach to establish the relationship between cognition and affect. Such affect-modulated cognition in animal studies is termed cognitive bias, which includes three classes: attention biases, memory biases and judgement biases (Crump et al., 2018). Attention bias studies aim to compare the attention given to different cues (usually positive or negative) and tie the measures of attention bias to the affective state which the animal could be experiencing (Ede et al., 2019). Memory bias tasks are based on the mood congruent

memory effect, which is an ability to better recall positive or negative events depending on the valence (whether it is positive or negative) of experienced affective state (Paul et al., 2005). While the use of attention and memory bias research in animals is relatively limited, judgement bias approach is considered to be the gold standard for measuring mood in animals (Bateson and Nettle, 2015). Judgement bias tasks are based on training animals to differentiate cues with a positive and negative outcome, and then presenting an ambiguous intermediate cue to them. If an observed response is more positive or negative rather than intermediate, then it can be concluded that the animal is optimistic or pessimistic (Ede et al., 2019). An example of using judgement bias approach for evaluation of pig welfare is the research of Douglas et al. (2012). In this study, 12-week old gilts were housed either in barren or enriched (with straw, manipulable object and higher space allowance) environments for five weeks, and trained to discriminate a positive (resulting in a food reward) and negative (resulting in a plastic bag being waived in the face) auditory cues. When an ambiguous cue was presented, pigs housed in the enriched environment were more responsive, which allowed to conclude that these pigs were more optimistic and hence had a more positive affective state.

There is evidence that chronic stress impairs not only the motivation for reward but also cognition (Kleen et al., 2006). Therefore, similarly to motivation studies, cognitive bias research can help to detect the presence of chronic stress. Cognitive bias studies provide an important tool for studying cognitive components of animal emotions and assessing emotional valence (positive or negative), but they also have potential limitations, such as the need for preliminary training of experimental animals, being time-intensive and the risk to influence the study results by researcher's actions, if the experiment methodology is not thoroughly developed. Overall, mood assessment research provides great opportunities for studying emotional states in pigs which helps to evaluate pig welfare. This approach has already been successfully used in some swine studies, however, further development of swine-specific methodologies with possible expanding the area of research by including memory and attention bias tasks is needed.

To sum up, evaluation of behaviour is an important part of pig welfare assessment, as it can help to answer the questions surrounding whether the animal is healthy and if it has what it wants in its environment: while the behavioural observations can provide some important information regarding pathological and pre-pathological health conditions, evaluation of learned responses

and mood assessment primarily deliver information about animal affective states (Dawkins, 2003).

2.4 Options to improve the welfare of stall-housed sows

2.4.1 Providing a greater freedom of movement: an option to improve stall-housed sow welfare?

Stall-housed gestating sows are experiencing not only significant space restrictions but also the lack of environmental enrichment or other stimulation (von Borell et al., 2007). These conditions severely limit the animal's behavioural repertoire and, together with feed restrictions, may result in an increase in the incidence of stereotypies (Rhodes et al., 2005; Marchant-Forde, 2010) and enhance corticosteroid levels, which indicates the presence of chronic stress (Koolhaas et al., 1999).

Thus, when trying to improve sow welfare through reducing the levels of stress in stall-housed sows, a complex approach which includes environmental enrichment provision, reducing chronic hunger, and improving sow comfort and reducing lameness, is required. That stalls are spatially restrictive is one of the greatest concerns they present for sow welfare: this concern is also reflected in the requirement included in the Canadian Code of Practice for the Care and Handling of Pigs (NFACC, 2014) regarding the need to provide stall-housed sows with a greater freedom of movement as of 2024. Consequently, it has been of interest to identify whether providing stall-housed gestating sows with a greater freedom of movement could improve their welfare. The most realistic options of providing a greater freedom of movement to stall-housed sows without making a transition to group housing include the introduction of turn-around stalls, reviewing the dimensions of conventional stalls and providing periodic exercise.

To date, only a small number of studies have been conducted to assess the welfare of female pigs in turn-around gestation stalls, and the results of these experiments are rather controversial. McFarlane et al. (1988) found that slightly narrowing the turn-around stall from 61 to 56 cm reduced turning frequency by more than 30% (from 12.9 turns/day to 8.9 turns/day), leading the authors to conclude that the need to turn around in pregnant gilts may be not particularly strong due to high discrepancy in the levels of space reduction and decrease in frequency to turn around. Bergeron et al. (1996) reported that bred gilts housed in turn-around stalls during the first trimester of gestation, where they could increase their available floor space by pushing on

one or both sides of the stall, had significantly reduced plasma cortisol concentration in comparison to gilts housed in conventional stalls during the same period. The authors connected this result to a decreased level of stress, experienced by the pigs housed in turn-around stalls. At the same time, gilts in turn-around stalls performed more stereotypic manipulations towards chains and stall bars in comparison to gilts kept in conventional stalls, which means that an opportunity to turn around may be not useful for reducing stress. The authors connected the increased performance of stereotypies more to the stress caused by noise, associated with the moving chains, than to the impact of the housing system. Such results may also be due to the specific design of the stalls used in this study, which allowed the animal to increase its available floor space only at the expense of its neighbour's space, so each of the animals was constantly disturbed by its neighbour's movements. Interestingly, the levels of blood plasma cortisol were lower in gilts housed in turn-around stalls than in gilts housed in conventional stalls, which might indicate that increasing the levels of chain manipulation was a successful strategy for coping with stress in turn-around stalls, as suggested by the authors. Alternatively, decreased cortisol levels could indicate the presence of adrenal fatigue (Wilson, 2014) due to stronger chronic stress experienced by gilts in turn-around stalls.

If the industry was going to keep the stall-housing system as a part of the production chain during the breeding stage of the production cycle for better sow management during this period, and also to prevent early embryo loss which might happen due to the stress of mixing into groups in early pregnancy (Morgan et al., 2018), then turn-around stalls could possibly be a better temporary housing option than conventional stalls. However, a study conducted by Dedecker (2011) revealed, that sows housed in turn-around stalls for the first 30 days of gestation and moved to group pens afterwards, performed more aggressive behaviour towards their pen mates if comparing to the sows housed in standard stalls for the first 30 days of pregnancy. The authors relate this increase in aggression to a flaw of turn-around stall design: the swinging gate of the stall, which was meant to allow sows to turn-around in the stall, also allowed for stronger and more frequent bouts of aggression between sows, as observed, but not recorded and analysed by the researchers. Sow immune function was also affected by the treatment. Animals housed in turn-around stalls for the first 30 days of pregnancy and then moved to groups had lower NK cytotoxicity and higher cortisol levels than those housed in standard stalls, and the sows kept in turn-around stalls throughout gestation had lower NK cytotoxicity, lymphocyte proliferation,

WBC count and neutrophil phagocytosis than those kept in standard stalls. Such results imply that housing sows in turn-around stalls may induce aggression-related stress in early gestation, which continued in mid gestation after mixing, and this would lead to the less stimulated and adaptive immune status of these animals in early and mid gestation. In conclusion, the author recommended not to house sows in turn-around stalls neither during the entire gestation nor for a shorter period prior to moving to group pens, as it may negatively influence welfare and immunity of the animals due to increased aggression levels related to the specific features of turn-around stall design.

Reviewing the dimensions of conventional gestation stall is another possible option to enhance sow comfort, and in turn, welfare. Intensive selective breeding over the past decades significantly altered the sow's body structure and measurements, whereas the size of gestation crate remained the same. Moreover, the rapid growth of the midsection in sows due to fetal development throughout gestation also increases their spatial needs (Dedecker, 2011). Li and Gonyou (2007) found that large sows made fewer postural changes compared to gilts when housed in the stalls of the same width (55, 60, or 65 cm), which suggests that bigger animals experience difficulties with changing their body position in relatively narrow stalls.

This problem could potentially be solved by the transition from the standard stalls to width adjustable gestation crates, as shown in recent studies. For instance, Zverina et al. (2015) reported that sows housed in stalls where the width was adjusted to achieve 2.5 cm space between sow and stall when lying in full lateral recumbence without simultaneously touching the sides of the stall, spent less time performing oral-nasal-facial (ONF) and sham-chewing behaviours than sows kept in standard stalls. Furthermore, Salak-Johnson et al. (2015) found that gestating sows housed in width adjustable stalls had lower lesion scores, comparing to those housed in conventional stalls, or group pens with free-access feeding stalls. However, sows housed in width adjustable stalls were sham chewing more frequently before and after feeding (from 0300 to 1500 h), than sows housed in standard stalls. This was explained as a consequence of a front gate design in the width adjustable stalls: the gates of these stalls contained vertical bars, limiting sow's ability to perform bar biting, so this pre- and post-feeding oral activity could be redirected toward sham chewing. However, there was no difference in the performance of ONF behaviours between sows kept in conventional and width-adjustable stalls, which was recorded and analysed separately from sham-chewing. It would be expected that the performance

of ONF behaviours should be lower in sows kept in width-adjustable stalls because of reduced bar biting, but the authors explained that it was compensated by more frequent manipulations with the top bar of the stall gate, which was the part of the width-adjusting mechanism. However, the levels of manipulation of the vertical bars and the top horizontal bar of the stall gate were not reported separately.

The evidence on the benefits of housing gestating sows in turn-around stalls and width-adjustable stalls for sow welfare is inconclusive. Nonetheless, such transitions to either turn-around or width adjustable gestation stalls would be financially demanding for the industry, so how much of a welfare improvement these systems offer needs to be thoroughly investigated prior to investment. Moreover, even if these housing systems were confirmed to effectively improve sow welfare, the public perception of turn-around stalls and width-adjustable stalls would most likely be negative. The results of a US public survey on pig farming practices showed that the biggest societal concern is housing pigs in close confinement (Sato et al., 2017), and while turn-around stalls and width-adjustable stalls offer more space for sows, this additional space is not sufficient to allow animals to walk and move freely, which is the societal expectation.

Periodically exercising gestating sows could be a cheaper option since it does not require any physical barn conversions. However, it is important to understand if this approach will really help to improve the welfare of stall-housed sows, which could be reflected in a reduction in stress, enhancement in productivity and reproductive performance, as well as piglet viability. Moreover, previous studies on providing a greater freedom of movement to stall-housed sows focused on physical, physiological measures and observation of behaviour, but motivational aspects of providing a greater freedom of movement have not been explored. It is important to determine whether gestating sows are motivated for periodic exercise at all, because if not, forced exercise may only enhance the stress levels for sows instead of reducing it.

2.4.1.1 The impact of periodic exercise on stall-housed sow physical, physiological and behavioural measures of welfare

To date, few studies exploring the impact of periodic exercise on gestating sow welfare have been conducted. Rather, the answer to confinement has been to provide ad-lib access to freedom of movement through group housing to offer the sow opportunities to have control over her

environment and to make choices. However, there are different factors that will influence the welfare of group-housed and stall-housed sows: for example, group-housed sows may experience an increased level of social stressors, e.g. aggression of pen-mates, and if an individual exercising strategy in stall-housed sows is applied, this factor can be excluded. However, if the sows have an opportunity for even minimal social contact with other animals during periodic exercising (e.g. exercise in an alleyway between the rows of stalls in a gestation room), while being in general socially stimulating, having this opportunity may also lead to the development of social stress in exercising sows, due to an inability to resolve agonistic encounters with other pigs, as it was shown in stall-housed sows, having a restricted social contact with their neighbours in adjacent stalls (Broom et al., 1995). Moreover, conditions under which sows are periodically exercised should also be taken into account when assessing their welfare: in most previous studies animals were walked by handlers, and moving forward was encouraged by the use of a board, taps from the hand or vocal cues. Such stimulation may result in higher levels of stress response in sows involved in these studies (especially if animals had a negative handling experience before and are afraid of humans) if comparing to the animals tested under the experimental design which would allow them to express a whole range of natural behaviours when exercising (voluntary exercise).

The results of the research related to the impact of periodic exercise on sow welfare conducted to date, rather confirm a hypothesis about the positive influence of movement on gestating sow well-being. There is some evidence that exercise could enhance the physical and psychological welfare of pigs. The physical well-being of an animal can benefit through the reduction of lameness and improving overall leg health, and these effects may be reached via providing access to exercise, as shown in several related studies. For instance, Perrin and Bowland (1977) reported that individually housed boars exercising on a treadmill from three to six 10-minute periods three times a week showed significantly fewer front leg abnormalities (bowleg and flexion of the carpus) than not exercised boars. In the same study, the degree of leg unsoundness in not exercising boars increased between two control visual appraisals with the 4-week interval, whereas in exercising boars it remained the same, which suggests that exercise may delay the onset of leg weakness. This result is possibly due to the positive effects of exercise on muscular, cartilage and bone strength, as no difference in joint lesion scores (which could affect leg soundness) were observed in this study. At the same time, the increased degree of leg

unsoundness (especially upright leg posture) if observed in sows, may shorten animal longevity (lifetime and removal parity; Nikkila et al., 2013). Palacio et al. (2016), in their study on the effects of regular exercise (access to pasture and winter exercise) in lactating Holstein cows housed in tie-stalls, found that during the winter months there were significantly lower lameness scores in the herds with exercise compared to herds provided with no exercise (18% vs 38% respectively). This could be explained by better blood circulation in the feet promoted by regular exercise, which provided claw tissue with nutrients and oxygen and removed possible toxins, preventing laminitis-related lesions (Loberg et al., 2004). However, in some cases exercising can also promote lameness, as demonstrated by the study of Morrison et al. (1968): the authors exercised gilts by running/walking 400 m in the alleyway twice a day, and reported that heavier gilts (averaging 60 kg) had a higher incidence of lameness than lighter gilts (averaging 50 kg). This finding suggests that body weight could contribute to lameness if the pigs are exercised periodically, probably due to increased claw horn wear rates and a higher risk of injury, related to greater pressure exerted per unit area of the claw as the bodyweight increases (Anil et al., 2007).

Schenck et al. (2008) reported that gilts, which were exercised for 2 hrs five days a week (low exercise group), took less time to lie down than those that did not receive any exercise (control group). Gilts that received exercise at higher levels (2 hrs for two days and 7 hrs for three days, five days per week in total: high exercise group), showed a higher speed of lying down in comparison to the low exercise group of gilts. Interestingly, preweaning mortality in both high and low exercise groups was lower than in the control group. In contrast, bone strength was higher in the low exercise group, than in high exercise and control groups. All the experimental animals were fed with an amount of feed based on their body condition (approximately 2.3 kg of feed one time per day), and during exercise they were encouraged to walk/run forward with light pats and vocal signals of a walker. Results of this experiment suggest that periodic exercise in gestating female pigs can improve sow health through its' positive impact on the musculo-skeletal system, which was represented by positive changes in lying behaviour and bone density. Moreover, the increase in the speed of lying down in the gilts receiving periodic exercise is related to enhanced muscle tone and suggests that these animals can better control the lying process. In turn, this may lead to a decrease in piglet crushing in the pre-weaning periods in comparison to non-exercised sows (Marchant and Broom, 1996).

As previously discussed, the lack of environmental stimulation in barren stalls may severely limit the sow's behavioural repertoire and result in enhanced corticosteroid levels, which indicates developing of a stress response (Koolhaas et al., 1999) and alter the behaviour by increasing the frequency of stereotypies (Rhodes et al., 2005; Marchant-Forde, 2010). Giving sows an opportunity for periodic exercise could help to reduce the monotony of the stall environment. However, it is important to consider the frequency at which exercise is provided: if it is very infrequent, the sow may perceive it rather as a frustrating factor (due to the stress of being in a new relatively unfamiliar environment, unexpected interaction with handlers, overall disruption of sow daily routine and possible muscle soreness after intensive infrequent exercise, which has not been studied in pigs) than as enrichment, so it would not have any beneficial effect.

Harris et al. (2013) exercised stall-housed sows in their first and second parities for 30 mins three times a week from mid to late gestation (from day 40 to day 104 (first parity), or to day 94 (second parity) of gestation). The authors evaluated sow behaviour and measures of fetal development, including fetal heart rate and vascular resistance indices for umbilical vessels (peak pulsatility index (PI) and resistance index (RI)), to explore the effects of periodic exercise on sow behaviour and fetal development characteristics. It was hypothesized that periodic exercise could reduce sow restlessness and improve blood flow to the developing fetus, which would positively affect sow physiology and performance, as well as piglet postnatal survival (due to decreased crushing). Indeed, it was found that the sows which received periodic exercise performed less restless behaviour (expressed as less sitting, more standing, lower tendency to lying and fewer postural changes), and reached PI earlier than the sows confined in stalls throughout gestation and not exercised. However, neither the PI, nor the RI was affected by maternal treatment, and fetal heart rate was affected only by a day of gestation. Indices of resistance (PI and RI) are inversely related to blood flow, which means that when blood pressure and blood flow to the fetus are low, these indices increase. Reaching an earlier peak PI in the group of exercising animals may also be beneficial because the decline of vascular resistance which follows this peak is increasing blood flow to fetus and nutrient exchange at the level of the conceptus. Changes in fetal heart rate would indicate the release of catecholamines as a result of fetal hypoxia stress due to increased oxygen consumption by the maternal organism during exercise (Lotgering, 1983). These outcomes imply that exercise positively influences sow

physiology, as determined by the decreased performance of restless behaviour, and improved fetal nutrition. However, the postnatal effects of sow exercise for offspring were not identified in this study. Reduced restlessness could potentially decrease piglet preweaning mortality related to crushing, but this parameter in the study of Harris et al. (2013) was not recorded. Improved fetal nutrition due to periodic exercise was assumed to improve piglet viability by increasing fetal size and piglet birth weight, but these effects were not observed. However, other useful predictors of piglet survivability which could deliver some information on the effects of altered indices of vascular resistance, such as piglet latency to stand and latency to reach the teat, were not measured.

Both of the above-mentioned studies on the impact of periodic exercise on sow physiology demonstrated that exercising stall-housed sows will bring benefits to their musculo-skeletal system. It can also be presumed, that duration of exercise will be positively correlated with the enhancement of muscular fitness in sows, which means that stall-housed sows, that receive enforced exercise at high frequency and duration will be fitter than group-housed sows, as they will move more. However, the frequency and duration of exercise used in these studies are not realistic for the industry to implement due to high labour costs. Hence, the benefits of exercising sows at lower duration and frequency schedules for the musculo-skeletal system should be considered. To date, no other studies on the effects of lower levels of exercise in gestating sows, than those conducted by Schenck et al. (2008) and Harris et al. (2013), as well as on the effects of voluntary exercise, have been made. However, such research was done in other species, but the results are rather contradictory. For example, Loberg et al. (2004) looked at four groups of tied dairy cows, which were: i) voluntarily exercising for one hour daily, ii) voluntarily exercising for one hour twice a week, iii) voluntarily exercising for one hour once a week, and iv) not having an opportunity to exercise. The results found that the duration of lying down movements between these group on the fifth month of treatment, as well as lameness score on the sixth month of treatment did not differ. However, animals from the exercise treatments were exercising simultaneously in a group paddock, which could affect their behavioural patterns and levels of activity.

Because the evaluation of animal welfare includes not only the evaluation of health and basic functioning but also the assessment of animal affective states, previous studies in pigs and other species also looked at motivational aspects of exercise to understand how animals feel

about being exercised. One of the indicators of the presence of strong motivation, as determined by Dawkins (1988), is the increased performance of a certain behaviour after a period of deprivation with a following decrease of performance. For example, Freire et al. (2009) studied the effectiveness of different types of exercise for fulfilling the need to exercise in horses. For this purpose, four groups of horses were assigned to the treatments which involved 40-60 mins of a certain type of exercise every day on days 1-4 of the study, and then 40-60 mins of forced restricted movement (being tied or kept in a relatively small enclosure) on days 6-9 of the study, so each animal was its own control. On days 5 and 10 each horse was separately released into a riding arena for 15 minutes for the rebound test and its activity was recorded. The authors reported that during the rebound tests on the day following exercise, horses from all treatments performed less walking, trotting and cantering than during the test on the day following the restriction of movement. These results indicate the presence of the rebound effect in horses from all treatments after being deprived of exercise for four days, which suggests that horses are strongly motivated for movement. At the same time, all types of exercise provided to the horses reduced the rebound effect, meaning that all the tested types of exercise can fulfil the need for movement in horses.

There is a lack of studies on the rebound effect in gestating sows, which would indicate the presence of an intrinsic need for exercise. However, it would be of interest to explore, especially considering the study of Rioja-Lang et al. (2013), which found that when giving sows the option to remain in the stall or to access a group area in the free-access stall housing system, they would spend over 82% of their time budget in the stall, suggesting that their motivation for exercise may be low. The right choice of the exercise strategy when exercising sows is also important: one might argue that controlled forced exercise would be beneficial for sow health, as it would impose more pronounced physical demand on sow body and lead to improved cardiovascular health and locomotory ability (Pedersen-Macnab et al., 2020). On the other hand, providing sows with voluntary periodic exercise giving them the freedom to explore surroundings gives them an opportunity to have control over their environment and to express natural behaviours (Pig Code of Practice Scientific Committee, 2012), which is important for sow mental state. An alternative strategy for periodic exercise is rewarding sows for exercise. This approach was used in the study of Schenck et al. (2008), where sugar cubes were provided to the sows once per lap to encourage them to reduce time spent in exploration, and in the study of Harris et al. (2013),

where sows were rewarded with a cookie at the completion of an exercise session. With this approach, sows presumably receive the same improvements of cardiovascular and musculoskeletal systems as from forced exercise, but also experience positive affective states from getting a reward. However, in this scenario it is difficult to evaluate the strength and the presence of sow motivation for movement per se.

All the above-described evidence suggests, that conducting species-specific research with the experimental design maximally close to the real production conditions is needed to fully evaluate whether providing periodic opportunities for exercise to stall-housed sows can bring positive welfare benefits and what exercise regime is optimal.

2.4.2 Providing enrichment and nutritional resources as an option to improve the welfare of stall-housed sows

According to Elmore et al. (2012, pg. 10), environmental enrichment can be defined as “biologically relevant additions or modifications to the environment that allow coping with stressors by promoting species-specific coping behaviours, and may be linked to positive affective states.” Due to swine instinct to test objects in their environment for edibility, the research on environmental enrichment for pigs is primarily focused on biological materials, such as straw, compost wood blocks and peat (Horback et al., 2016). The use of inexpensive natural enrichment materials is particularly relevant to stall-housed sows, as enrichment must be provided to each individual gestational stall, which may be too costly for farmers if using commercially manufactured enrichment. In feed-restricted gestating sows, fibrous foraging and rootable materials, such as straw and mushroom compost, may serve not only as an occupational and recreational enrichment, but also as a nutritional enrichment, acting as a secondary feed source, and transform sow feeding motivation into foraging behaviour (Verdon et al., 2015).

Numerous studies conducted in group-housed dry sows confirm their motivation to get access to rootable and foraging substrates, and the impact of access to this enrichment on sow behaviour and nutritional status. For example, a study conducted by Elmore et al. (2011), confirmed sows’ willingness to interact with foraging enrichment substrates. It showed that group-housed gestating sows when getting access to the pen enriched with multiple enrichment sources, were more motivated to interact with straw and compost in comparison to cotton ropes. Similarly, Roy et al. (2019) demonstrated that group-housed gestating sows were interacting with

straw more frequently than with cotton rope and hanging wood block enrichment if these three enrichments were rotated with or without the associative stimulus signaling the arrival of enrichment (a bell or whistle). Interestingly, when studying gestating sow preference for hanging ropes, hanging rubber sticks and fixed wood blocks but without access to straw, Horback et al. (2016) discovered sows interacted with cotton ropes more often than with rubber sticks and wood blocks. The authors related this finding to sows having an opportunity to perform highly motivated foraging-related behaviours, such as chewing and pulling, when interacting with ropes. Spooler et al. (1995) also found that group-housed gestating sows, when offered multiple sources of enrichment, spent more time on interaction with the straw, directing their foraging behaviour towards it, than on chain and bar manipulations, which were regarded as stereotypic behaviours. In contrast, Stewart et al. (2008) did not find any effect of introducing straw racks to dry sows in large dynamic groups on levels of sham chewing behaviour. However, the sows in the same study showed reduced exploratory behaviour, which could be related to increased satiety level.

Fewer studies explored sow desire to access enrichment in stalls, however, the results of these studies are similar to those obtained from group-housed sows. For instance, motivational studies conducted by Elmore et al. (2012) in stall-housed gestating sows prove that animals housed in barren stalls value access to such foraging substrates as straw in a rack and compost in a trough, as indicated by lower latency to press the operant panel and higher operant responding to access compost in comparison to the negative control (empty trough), and a higher percentage of time spent in interaction with straw, in comparison to food, compost and empty trough.

Despite the existing solid scientific evidence on the value of providing foraging and rootable enrichment to gestating sows, the disadvantages of this type of enrichment, such as higher production costs (e.g. due to increased costs of materials and labour), and incompatibility with existing infrastructure, e.g. slatted flooring and liquid manure systems (Tuytens, 2005; Elmore et al., 2011), significantly limit the use of these resources in commercial barns.

Incorporating high-fibre feed in a sow diet also helps to reduce feed motivation (Verdon et al., 2015), as indicated by reduced sow activity and reduced performance of self-directed behaviours. For example, de Leeuw et al. (2004) have shown that including of high levels of dietary fibre (sugarbeet pulp) in a standard ration of breeding sows induced a long-lasting feeling of satiety, which was characterized by more stable glucose and insulin levels, as well as reduced

physical activity several hours after feeding compared to sows receiving lower levels of dietary fibre. Ramonet et al. (1999) also demonstrated that pregnant sows fed a high-fibre diet spent less time standing in comparison with sows fed a conventional low-fibre diet. Similarly, studies conducted by Zonderland et al. (2004) revealed that sows, fed with an ad libitum amount of high-fibre diet, showed less activity in comparison to those fed with a restricted amount of a low-fibre diet. Further, de Leeuw et al. (2005) reported that performance of self-directed behaviour in gestating sows, which, according to Zonderland et al. (2004), serves as a behavioural indicator of satiety, decreased as the level of high-fibre sources in the diet increased.

To sum up, previous research has demonstrated that gestating sows value having access to foraging enrichment and that high-fibre feed provision increases satiety in feed-restricted sows while maintaining the desired energy intake levels. Therefore, providing fibrous enrichment and high-fibre feed are considered to be viable options to improve sow welfare in stalls.

2.5 The impact of periodic exercise on stall-housed sow reproductive performance and piglet development and viability

2.5.1 Sow reproductive performance characteristics

There are numerous studies that explored the productivity benefits from group-housing of gestating sows, explained by improved sow fitness due to higher levels of movement in groups in comparison to stalls, and also by reduced levels of stress in the group pens because of having more opportunities to perform innate behaviours when having access to a greater freedom of movement and due to having some control over the environment. Sow reproductive performance includes both fertility and prolificacy (number of piglets born alive; Koketsu et al., 2017). Early embryonic loss, which is a major limitation for increasing sow prolificacy (Geisert and Schmitt, 2002), happens during the second to third week of gestation and can be related to asynchrony in embryonic development relative to uterine development, followed by placental attachment abnormalities. Uterine secretory activity, which is responsible for the development of the uterine environment, is controlled by maternal hormones (Fischer and Beier, 1986). Later fetal losses (25-45 days of gestation), leading to low sow prolificacy, can happen due to limitations in uterine capacity, which is defined as an ability of the uterus to provide necessary nutrients to maintain fetuses until farrowing and can be measured as the number of piglets born alive when the number of embryos is not limited (Freking et al., 2016). Placental characteristics can also

impact prolificacy. According to Smith and Fretts (2007), in humans most stillbirths are related to placental dysfunction, which is associated with fetal growth restriction. In swine, fetal growth restriction may occur when the placenta is relatively large, due to a limited fetal growth capacity or to a restriction of placental functioning (van Rens et al., 2005). Sow prolificacy and productivity may also depend on other placental traits: according to Baxter et al. (2008), such placental traits as areolae density and a total number of areolae are directly associated with the fetal death levels, which in turn are negatively correlated with the number of piglets born alive. However, the same study showed no impact of other placental characteristics, such as placental efficiency (ratio of birth weight to placental weight), total litter placental and individual placental weight, placental vascularization and surface area, on prenatal survival. These results suggest that the level of development of placental areolas is one of the determinative factors of prenatal piglet survival, whereas placental size rather does not have a positive impact on fetal growth. Interestingly, farrowing intervals in this study did not affect the survival rates, even though it is considered that shorter farrowing intervals may decrease the number of stillborn (Lammers et al., 2007).

Human medical research found some evidence of a positive influence of exercise on fetoplacental growth, resulting in faster placental development and improved placental function (Clapp et al., 2000). This study showed that placental volume and placental growth weight were higher in women performing weight-bearing exercise for 20 mins from three to five times per week throughout pregnancy than in those not exercising at the same period. Moreover, placentas of exercising women contained less non-functional tissue and a greater volume of villous tissue, which plays important role in fetal metabolic exchange and circulation. It implies that the impact of exercise on placental development characteristics should also be taken into account when analyzing reproductive performance and productivity measurements.

Numerous studies, conducted in stalled and group-housed gestating sows revealed a correlation between the system of housing and sow fertility, prolificacy and productivity. For example, Lammers et al. (2007), in a study which included 353 sows and 957 litters, found that sows gestating in deep-bedded group pens had better prolificacy, giving birth to more live piglets per litter, than sows housed in stalls throughout gestation. The author suggested that a greater opportunity to move given to gestating female pigs can produce an improvement of overall and uterine muscle tone, which leads to a decrease in the number of stillborns. In contrast, sows

which were stalled throughout gestation returned to estrus sooner than sows housed in group pens. This may be due to the increased levels of social stress in group-housed sows in comparison to individually housed animals. However, such results may also be caused by the presence of straw in the experimental pens, which was serving as nutritional and environmental enrichment. The sows likely were consuming their straw, which could influence the litter size, as ingesting dietary fibre has previously been demonstrated to improve embryo survival in swine (Jarrett and Ashworth, 2018). Also, sows housed in bedded pens could move more when interacting with the straw, if compared to the sows in barren group pens or in stalls, which could improve their overall and uterine fitness (Tuytens, 2005). In contrast, a study conducted by Fulawka (1996) demonstrated, that there was no significant difference in the litter size, piglet birth weight, weaning to estrus interval and pregnancy rate in pregnant gilts, housed in groups of three or four in conventional pens and gilts, housed in a group of 30 in a straw-bedded pen. However, these outcomes also may be due to the difference in the levels of social stress: high levels of social stress in the bedded pen could be reduced by the presence of enrichment, whereas the levels of environmental stress in barren pens could be balanced by reduced levels of social stress, as the group size was smaller.

On the other hand, Weng et al. (2009) reported that stalled sows had a longer interval between puberty and second estrus, and a longer interval for rebreeding after weaning, in comparison to group-housed sows, which contrasts with the findings of Lammers et al. (2007). However, the sample size in the study of Weng et al. (2009) was much smaller (80 gestating female pigs in total), which could be an explanation for this discrepancy. Such results may also indicate the difference of individual herd performance and management in these studies. Furthermore, even though the authors did not find a significant difference in total litter size between gestation treatments, they reported a significantly higher number of stillborn piglets in the stall treatment, which is in agreement with the results presented by Lammers et al. (2007).

Similarly, Chapinal et al. (2010) revealed a lower number of piglets born dead per litter in sows, housed in groups with an unprotected electronic sow feeder, than in groups with trickle feeding, or in stall-housed sows. Tan (2015) also showed that sows housed in groups had a greater number of piglets born alive compared to the sows housed in stalls.

Such consistent results of reduced levels of stillbirths in group-housed female pigs in comparison to stall-housed ones may be due to shorter farrowing intervals in group-housed sows,

related to improved overall and uterine muscle tone in animals which received exercise. Another possible reason is a positive effect of movement throughout gestation on placental development. However, the true reason remains unknown, as none of the above-described studies looked at these characteristics.

Studies on periodic exercise in gestating sows have also shown some impact of giving a greater freedom of movement on sow reproductive performance, productivity and placental characteristics. Harris et al. (2013) found an increase in umbilical blood flow in stall-housed sows in their first and second parity, which were exercised for 30 minutes three times a week (from 40 to 104 days (first parity) or to 94 days (second parity) of gestation), suggesting that periodic exercise could have a positive impact on reproductive performance in gestating sows through bringing a greater volume of oxygenated and nutrient-rich blood to the fetal systemic circulation. However, the same study did not reveal any effect of exercising on placental weight.

Kaminski et al. (2014) demonstrated that providing stall-housed sows in their first and second parity with periodic exercise at the same frequency and duration as described by Harris et al. (2013), from day 40 to day 104 of gestation in their first parity, or to day 94 in their second parity, resulted in increased cell proliferation in fetal ovaries and ovarian weight in the group of lightest neonates. The authors explained it as a consequence of increased umbilical blood flow in sows receiving exercise, which benefitted the development of piglets in general and enhanced their chances for survival.

Giving sows an opportunity to exercise at frequencies described by Schenck et al. (2008) did not impact the number of piglets born alive, as well as the total number of piglets born and the percentage of stillborn, in comparison to stall-housed non-exercised animals. In this study, the animals were fed with an amount of feed based on their body condition (approximately 2.3 kg of feed one time per day), and during exercise they were encouraged to walk/run forward with light pats and vocal signals of a walker. It may suggest that exercising for such long periods and at a high frequency is of no use not only because of the costs of required labour but also due to a lack of improvement in sow reproductive performance and productivity when exercised at high rates, in comparison to exercising at lower rates.

2.5.2 Piglet development and viability measurements

Piglet birth weight, ponderal index, body mass index, farrowing birth order (piglets being born later in the birth order are more likely to be born dead), rooting response (the vigour the piglet uses to root at the udder and massage the teats), as well as latency to suckle, are good predictors of piglet survival and can be successfully used to assess piglet vitality (Baxter et al., 2008). Muns et al. (2013) found that performing udder stimulation movements or searching behaviour together with an ability to turn its body axis 360° from its initial orientation or walk along the limits of the bucket at least twice in the 30-s test within three hours after the end of farrowing, are influencing piglet survival during lactation, which is related to piglet neonatal vitality (Baxter et al., 2008). Prewaning mortality levels can also be used as an additional measurement of piglet survivability.

Most studies comparing stalled and housed in different group systems pregnant sows conducted to date did not confirm a hypothesis about the positive impact of maternal exercise during gestation on offspring characteristics. However, piglet viability was not an area of interest in these studies, so they recorded only piglet birth weight, not taking into account any other piglet survival parameters.

Chapinal et al. (2010) did not find any significant difference in the total weight of piglets produced, as well as in the total weight of piglets born alive between stalled, group-penned with an unprotected ESF (20 animals per pen, space allowance 2.32 m²/pig), and housed in groups with trickle feeding in feeding stalls (10 animals per pen, space allowance 2.76 m²/pig), female pigs. Similar results were reported by Hulbert and McGlone (2006), who compared litter birth weight from the gilts housed in groups of five in pens with feeding stalls (space allowance 1.32 m² per pig) to gilts housed in individual stalls. Harris et al. (2006) also demonstrated that there was no significant difference in individual piglet birth weights and litter birth weights between gilts housed in individual stalls and groups of four with feeding stalls and space allowance of 2.4 m² per sow. In contrast, Seguin et al. (2006) reported higher piglet birth weights in group-housed sows (groups of 11 to 31 sows with floor feeding, space allowance 2.3 m², 2.8 m² or 3.2 m² per sow) than in stall-housed dams. Sorrells et al. (2006) also observed that piglets from gilts housed in groups of four with the space allowance of 2.34 m² per sow and feeding stalls during gestation were heavier at 35 days of age in comparison to those born from stall-housed gilts. Additionally, Lammers et al. (2007) did not find any differences between the housing treatment (individual gestation stalls or deep-bedded group pens) and preweaning mortality.

As can be seen, the results of the above-mentioned studies are very heterogeneous and do not reveal any connection between piglet birth weights, space allowance and feeding system, which does not allow to assess approximate levels of sow movement in these studies and compare them to the measures of piglet viability.

Results obtained from the experiments on the influence of periodic exercise on piglet traits were more consistent. Schenck et al. (2008) observed that a high-intensity regime of periodic exercise (two hours for two times and seven hours for three times a week) from mid to late pregnancy resulted in enhanced piglet body weight at birth and lower preweaning mortality if compared to the litters from the sows receiving no or less exercise (two hours for five days per week). A study on frequent periodic exercise (30 minutes three times a week) in pregnant sows of first and second parity, conducted by Harris et al. (2013) did not show any significant impact of having access to a greater freedom of movement in gestating dams on offspring birth weights and farrowing intervals. The same results for the piglet birth weight were reported by Kaminski et al. (2014).

Larger piglet birth weight and lower preweaning mortality in the sows receiving exercise at high frequency and duration may be related to increased umbilical blood flow, which means a better supply of nutrients to the developing fetus and it may be linked to better development of placental areolas. Unfortunately, these parameters were not assessed in the study of Schenck et al. (2008), so the future investigation is needed. It also can be presumed that the increase in umbilical blood flow in sows exercising at a high-intensity regime will be significantly higher than that reported by Harris et al. (2013), as in the latter study it did not impact piglet birth weight.

To sum up, periodic maternal exercise may be a possible option for enhancing beneficial piglet characteristics, but achieving the levels at which it needs to be applied to get significant improvements, may be challenging for the industry.

2.6 Conclusions

Stall confinement throughout gestation may have significant negative consequences for sow welfare, and if the sow is stressed in the stall, it is likely that this type of gestation housing could contribute to the development of chronic prenatal stress. Similarly, sows housed in groups experience different stressors that may result in the development of chronic stress. However,

most of the work to date has looked at more acute measures of stress. At the same time, there are methods that may be better suited to study the welfare of gestating sows as they help to assess chronic stress levels, such as evaluating the effects of the housing system on piglet viability and characteristics. Since the dam is pregnant, PNS is affecting not only the sow but also her subsequent offspring, which may have particularly detrimental outcomes. However, even though being widely studied in humans and laboratory animals, the effects of PNS in gestating sows are not completely understood. The majority of recent studies cast a doubt on the significance of the impact of chronic stress on productivity in female pigs, but the interpretation of these results should be careful due to high variation and weaknesses of the experimental designs used. Results of the studies on the viability of prenatally stressed piglets are rather conflicting and also need an adequate assessment, considering the results of exposure to naturally induced stress more reliable than those obtained from the animals which received hormonal treatment.

Further research on the origins and levels of prenatal stress in stall-housed gestating sows is needed, as this data would help to identify if some management practices need to be adjusted to better manage the stress for the sow, to reduce adverse effects on the offspring. If a positive impact of periodic exercise on sow welfare is confirmed, implementation of this approach would result in, on the one hand, lower financial and labour costs in comparison to other options of PNS reduction, and, on the other hand, decreasing the levels of PNS in sows through meeting their physical, physiological and behavioural needs without any excessive social pressure.

Providing exercise to the stall-housed sow is a novel approach. To date, most of the studies have simply investigated how group gestation housing, which provides the sows with complete freedom of movement, impacts sow basic health and functioning, behaviour, reproductive performance and piglet characteristics. The results of these experiments are very heterogeneous: they imply that giving a greater opportunity of movement to pregnant sows is positively correlated with improvement of sow health status, as well as behavioural and reproductive characteristics, but it is hard to evaluate this relationship due to a high variety of research objectives, methods and experimental designs.

It seems to be even more difficult to draw any certain conclusions about the role of periodic exercise in relieving gestational stress in female pigs, due to an extremely small number of studies conducted on this topic to date. Results of these few experiments suggest that periodic exercise may be a possible option for improving sow health, physiology and reproductive

performance. However, further research is needed to effectively evaluate the effects of periodic exercise on these parameters. Moreover, to be able to correctly evaluate the levels of welfare in periodically exercised sows, sow affective states also need to be assessed, and while previous research looked at some basic health and functioning aspects of periodic exercise, none of the conducted to date studies evaluated how sows feel about being exercised and whether providing periodic exercise benefits sow mental state. Providing periodic exercise was proposed as an option that would be more favourable for sow welfare, but it is important to verify whether it can provide the level of welfare which is equal to that provided by housing in groups. It is also important to determine whether giving the sow an opportunity to have a greater freedom of movement for brief periods at a lower frequency that the industry may be able to implement, is beneficial to the sow, because exercise provision at the frequency and duration tested in previous studies is not likely to be achievable in commercial practice.

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3. MOVEMENT OR MORE FOOD? A COMPARISON OF MOTIVATION FOR EXERCISE AND FOOD IN STALL-HOUSED SOWS AND GILTS

This chapter presents an operant conditioning study conducted to compare motivation for food and movement in stall-housed gestating female pigs as the first step of investigation of whether gestating female pigs value having access to a greater freedom of movement and whether providing periodic exercise can improve gestating sow welfare. It was found that sows had a greater motivation to access feed than exercise, and gilt and sow motivation to access movement did not differ.

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Abstract

Despite being phased out in the EU, several states in the USA and other select countries such as Australia, gestation stalls remain a common sow housing system worldwide. In Canada, the 2014 Code of Practice for the Care and Handling of Pigs permits the operation of existing stall barns, provided that bred female pigs are given opportunities for a greater freedom of movement, such as access to periodic exercise. How stall-housed sows perceive being confined and whether they are motivated for a greater freedom of movement has not been investigated. The objectives of this study were to determine the motivation of bred female pigs with different prior stall experience (PSE; gilts or sows) to receive access to an alleyway for three minutes (Movement), and to compare this to their motivation for a feed reward (Food: 0.2 kg per reward). Stall-housed gilts ($n = 12$) and sows ($n = 12$, parity 2-4) were trained to use an operant panel with two buttons: an active button (AB – push counts resulted in a reward of feed or movement), and a dummy button (DB – push counts not rewarded). Animals were tested on an ascending fixed ratio (FR), with the required number of AB presses increasing by 50% each consecutive day. Upon reaching their individual maximal FR for one reward, animals were retrained and tested on the opposite button and received the alternate reward. The maximum AB push count achieved during a testing session, the highest price paid: HPP, was used as a measure of sow motivation for the reward. Animal behaviour when out of the stall and the percentage of AB presses were also recorded. The HPP was influenced by PSE and reward type. Sows showed a greater HPP for feed than movement, but for gilts it did not differ. Sows had a greater motivation to access feed than gilts, however, gilts and sows did not differ in their motivation to access movement (mean HPP \pm SEM, sows Food: 369.25 ± 56.47 vs Movement: 68.5 ± 13.61 ; gilts Food: 211.67 ± 47.73 vs Movement: 77.75 ± 19.47 ; $F_{1,44} = 4.23$, $P = 0.046$). Results suggest that stall-housed gestating sows and gilts are similarly motivated to access time out of their stall. The presence of the motivation for movement is important for sows even though they had a greater motivation to access a feed reward, and the motivation for a feed reward increases with PSE.

Keywords: Pig, Operant conditioning, Gestation stalls, Exercise, Welfare.

3.1 Introduction

The welfare of stall-housed gestating sows remains a point of concern (Yunes et al., 2018). Gestation stalls are criticized for physically and socially restricting sows and therefore not

providing adequately for sow welfare. In response to this concern, multiple countries have fully or partially phased out gestation stalls (von Keyserlingk and Hotzel, 2015).

In Canada, the 2014 Code of Practice for the Care and Handling of Pigs requires that all new buildings and barn renovations must house bred female pigs in group-gestation pens. The Code also permits that as of 2024, stall-barns still in good working order may continue to operate, if female pigs are periodically given the opportunity for greater freedom of movement (NFACC, 2014). There is limited scientific evidence to understand how providing periodic access to greater freedom of movement will improve sow welfare, but this must be understood to ensure requirements for animal care will support animal welfare improvements.

One approach to providing a greater freedom of movement is to release sows from stalls periodically and allow them to exercise in the barn alleyways. The sow will gain physiological benefits when a higher level of exercise is provided: previous studies showed that periodic exercising increased lying down speed and bone strength, decreased the performance of restless behaviour and increased umbilical blood flow in gestating gilts (Schenck et al., 2008; Harris et al., 2013). However, providing the level of exercise used in these studies on commercial farms would be impractical; whether less regular exercise routines could bring any benefits to sow welfare needs to be understood. It is also important to explore if sows value access to periodic exercise, as animal feelings are an important aspect of welfare (Fraser et al., 1997).

Preference or motivation tests offer one approach to asking animals about the conditions being provided to them. In these tests, animals are given some control over their environment, and their choices and decisions are observed and analysed (Kirkden and Pajor, 2006a). Dawkins (1988), identified four criteria that indicate the presence of strong motivation: 1) performing the behaviour as a vacuum activity when the target resource is not present; 2) showing high levels of the behaviour after a period of deprivation from performing this behaviour (rebound effect); 3) signs of frustration (stereotypies, displacement) if there are no opportunities for performing the behaviour; 4) willingness to pay a high “cost” for an opportunity to perform a certain behaviour. Based on consumer demand theory, motivation tests measure an animal’s willingness to maintain the rate of consumption of resources when the cost per unit of resource increases (Dawkins, 1983; Kirkden and Pajor, 2006a). Tests of this type have previously been used to determine the motivation of stall-housed sows to access enrichment (Elmore et al., 2012), and to access a fully-slatted group housing pen (Kirkden and Pajor, 2006b).

An operant testing technique with an increasing number of responses required to access a resource gives the opportunity to directly determine the motivational strength by measuring the highest schedule that the subject completes (highest price paid; Kirkden and Pajor, 2006a). There is also a need to determine how the effort made by animals relates to the degree to which they need the resource. To standardize the effort performed by pigs when offered different resources, a food-metric scale was developed by Patterson-Kane et al. (2011). The benefit of this approach lies in utilizing a resource of known high value (food), which is a fundamental biological need, as a comparator. This comparison helps to effectively determine the animal's motivation to access a resource of unknown value.

The aim of this study was to determine the motivation of stall-housed gestating female pigs with different prior stall experience (PSE: gilts and sows) for access to greater freedom of movement. Motivation was evaluated by measuring the animal's willingness to interact with an operant panel to access greater freedom of movement and comparing it with its willingness to "work" for food. To better understand sow's motivation for access to greater freedom of movement, another objective was to analyze the behaviour of the animals when out of the stall. It was hypothesized that the motivation of female pigs for food would be higher than that for movement, and hence the highest price paid (HPP) as determined from the total number of active button presses made to the panel, would be greater for food than for movement. It was also hypothesized that the HPP for movement would be intermediate in comparison to HPP for food and negative control and, that the motivation for movement would differ between animals with different PSE.

3.2 Materials and methods

All experimental procedures were approved by the University of Saskatchewan Animal Care Committee (#20170057), which is regulated by the Canadian Council of Animal Care (2009). This experiment was conducted daily between November of 2017 and January of 2018 at the Prairie Swine Centre, Saskatoon, Canada.

3.2.1 Animals and husbandry

A total of 32 Camborough 42 (PIC genetics) pigs were studied. Stall naïve gilts (n = 12) and stall experienced sows (n = 12, parities 2–4, 3.25 ± 0.83 parities, mean \pm standard deviation

[SD]) were trained to interact with an operant panel to obtain a reward (experimental animals). An additional group of multiparous sows ($n = 8$, parities 1–6, 2.13 ± 1.96 parities, mean parity \pm SD) were not trained to interact with the operant panel for a reward and were used as a control measure (control animals).

All animals were bred and kept in stalls (2.1 m x 0.62–0.73 m) and remained on trial until they completed their own testing schedule. To work in line with the barn production flow, the animals were selected at 7–10 days following breeding. A total of four experimental animals (two gilts, two sows) were selected within one breeding week, forming one replicate block, with a total of six replicate blocks. Body condition score (BCS) was determined and recorded for each animal upon entry to the trial, which coincided with the first day of the operant panel training. Control animals were randomly selected within the same first four breeding weeks as the experimental animals (two sows per week). Sows were fed a standard pelleted ration containing 2.25 Mcal/kg, 11.96% crude protein and 4.55% crude fibre once a day at 07:00 h. On average the sows were receiving 2.3 kg of feed daily, with meal quantity adjusted to the body size and age, so large older sows were receiving up to 2.5 kg of standard gestation ration, and gilts were receiving approximately 1.9–2.2 kg of standard gestation ration, depending on the body condition. The feeding regime was kept constant during the study. When sows were trained and tested to press the operant panel for access to more feed, they were fed only 70% of their standard gestation ration in the morning. Thereafter, a handful of gestation feed (0.2kg) was provided as the reward, providing the sow with the remaining percentage of her feed ration over the course of testing. Any feed not consumed by the sows during testing was fed to sows once all training and testing were complete, ensuring that sows continued to get their full daily ration. To reduce the time effect of testing, the order of training and testing of individual sows within each replicate block was randomised each day. Each individual stall was equipped with a nipple drinker.

3.2.2 Experimental apparatus

An operant panel with two identical buttons (Fig. 3.1) was used to measure animal motivation. Both buttons could be programmed by a microcomputer to count the number of presses made. One button was designated as an active button (AB), and push counts to this button resulted in a reward for the sow. The other was designated as a dummy button (DB),

acting as a control measure, and press counts made to this button did not contribute to obtaining a reward for the sow. A metal divider separated the two buttons ensuring animals had to make a defined choice. An LED light positioned above, and centrally between the buttons was constantly lit when the panel was active (supplied with power and able to record button push counts). The light flashed and then turned off once the required number of button presses was reached. The light turned back on once the panel was reset for activation again. An additional light that followed the same sequence described was visible to the research staff on the control box that contained the microcomputer. The operant panel was presented to sows by hanging it inside the front gate of their stall. Power was supplied to the operant panel via a lithium battery pack. All button push counts were recorded on a microcomputer and the number of AB push counts required for the sow to retrieve a reward could be programmed into the microcomputer.

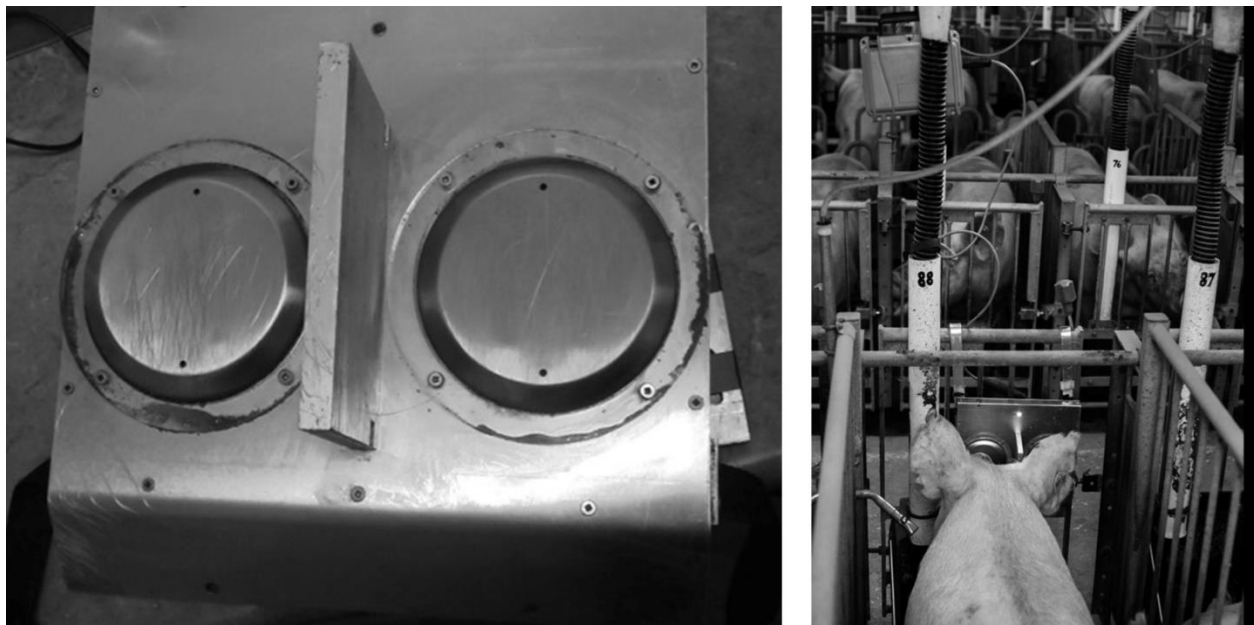


Fig. 3.1. The operant panel containing two identical buttons, a central divider, and a light to indicate when the panel is active; the image shows the inactive panel (left). Sow pressing the active button of the operant panel (right).

3.2.3 Experimental procedure

Sows were given their daily gestation food allowance in the stalls at 07:00 h each morning in accordance with farm practice and were allowed 1h to consume their meal. Training and testing of all animals on trial took place from 08:00 h to 14:00 h each day. Each animal was

awarded access to the operant panel for a total of 30 minutes per training/testing session. To associate the buttons with different operant responses, animals were trained to press one of the buttons for one reward, and after completing the testing schedule for this reward animals were retrained on the opposite button (switching the function of the AB and DB) for a different reward. Order of button training was swapped per replicate, and order of training/testing for different rewards was swapped per replicate as well to control for the effect of prior training experience (PTE).

Prior to testing, all animals were trained over the course of three days to press the AB up to a total of nine times, with three consecutive training opportunities within each 30-minute training session. On day one animals were required to reach the fixed ratio (FR) of 1 three times consecutively, and on day two animals were required to reach the FR of 3 three times consecutively. Animals that failed to meet the training criteria (reaching the FR of 3, 6 and 9 in consecutive presentations) on day three were awarded two additional days to meet the criteria. Animals that met the training criteria moved on to testing. When training and testing for access to exit the stall, sows were rewarded for pressing the AB with three minutes of time to freely move around within the alleyway between stalls. To receive this reward, the sows were let out of the stall. For this, the human handler opened the front stall gate fully, and stood out of the way, and out of view of the sow exiting the stall. The sow was left to exit the stall by herself. There was no human-animal interaction. The alleyway was swept every morning before the beginning of testing to remove any spills of feed. The barn room, used for the experiment, was designed in a way that when being in the alleyway, experimental animals had access to social interaction with other sows through the bars of their front stall gates.

Once trained, sows were tested on an ascending FR schedule, where the number of AB button presses required was increased by 50% each day after starting at FR 9, up to a maximum FR of 365. This produced a testing schedule of FR 9, 14, 21, 32, 48, 72, 108, 162, 243, 365. The maximum FR was established based on previous literature demonstrating the level of operant responding performed by sows following 23 hours of feed deprivation (Patterson-Kane et al. 2011).

Per the 30-minute testing session, each animal was given a maximum of three consecutive opportunities to reach the required FR and obtain its reward. Should an animal fail to reach the required FR within the 30-minute period, no reward was given. The animal was then given a

second opportunity to reach the required FR the following day, upon which if the animal reached the required FR, testing continued along with the schedule. If the animals failed to reach the required FR for a second day, testing ended. The following day the animal was retrained for their second training and testing session (exercise or food) and the process was repeated. For training only, to assist animals in understanding the position of the active button switch during retraining, a small amount of jam was applied to the AB to attract sows to contact the correct button. After the animal had completed testing for the second resource, the animal was off trial. Any animal that met the FR of 365 was presented with the panel for one additional day and the maximum number of AB presses the sow made within a 30-minute period was recorded (extinction).

The highest price paid (HPP) was defined as the maximum AB push count achieved by a sow over the whole testing session. As an indicator of sow motivation for the resource, it was recorded for each reward for every single sow. Latency to make the first AB push in the session when the HPP was reached, was recorded as an additional measure of motivational strength (Elmore et al., 2012).

Preliminary studies revealed that as the FR increased, the sows would begin to press the DB an increasing number of times. Therefore, a percentage of AB presses was calculated and analysed as an auxiliary measure of motivation and sow learning abilities, as well as the frequency at which sows pressed the panel.

The control sows who were not trained to use the operant panel, were presented with the panel for 30 mins on six consecutive days, and the number of AB and DB presses within each session was recorded.

3.2.4 Behavioural observations

A video camera (Sony HDR-CX405, Sony Corp., New York, NY, USA) mounted on the wall at one end of the alleyway into which sows exited, recorded the behaviour of sows once out of the stall for three minutes (Table 3.1). The total duration of time (s) each sow spent in exploratory behaviour, snout to snout contact, locomotor behaviour (total of durations of walking, trotting and running/scamper) and other (the total duration of licking bars and time out of sight of the camera) were calculated.

Similar to Goumon and Spinka (2016), a 15% sample of all video recordings was rewatched by the same observer to determine intrarater reliability (IRR). The following intraclass

correlation coefficient (ICC) values were obtained: 0.835 for locomotor behaviour, 0.965 for exploratory behaviour, 0.974 for snout to snout contact and 0.905 for other behaviours. Results with ICC > 0.8 were considered as good, and with ICC > 0.9 as excellent.

Table 3.1. Behavioural descriptions for assessing sow activity outside the stall.

Category	Behaviour	Description
Locomotion	Walking	The animal is moving at a slow pace, and always has two or three feet on the ground at any one time.
	Trotting	The animal is moving at a quick pace, between a walk and a run, in which legs move in diagonal pairs in a two-beat diagonal gait.
	Running/scamper	The animal is moving at a pace faster than walking and trotting. Running is represented by a controlled three-beat gait. Scamper includes hopping with both hind legs moving in unison.
Social	Snout to snout contact	The animal has a snout to snout contact with another sow through the gate of the stall.
Exploration/ foraging	Exploratory behaviour	The animal is exploring the environment (travelling forward or backwards with a snout on the ground, either in the centre of the alley or along the stalls. The sow may be standing, or kneeling and/or trying to place head under the bottom bar of the stall gate and reach feed inside the stall); eating if feed was reached.
Other	Licking bars	The animal is licking bars of the gate of an empty stall.
	Out of sight	The animal cannot be seen.

3.2.5 Statistical analysis

Data were analysed with the statistical package SAS 9.4 (SAS Institute, Cary, NC, USA). The significance level was set at $P \leq 0.05$. Results with $P < 0.10$ were considered as statistical trends. Residuals of all dependent variables were examined for normality and homogeneity of variances, and the data were transformed as necessary. The least-square means (LSMEANS) of fixed effects with Tukey's adjustment were used to account for multiple comparisons. The values in the text are presented as the mean \pm standard error of the mean (SEM) from the raw (not transformed) data as computed from the final model.

3.2.5.1 Motivation measures

To determine the influence of reward type and PSE (sow or gilt) on the HPP (maximum AB push counts over the whole testing session) and latency to make the first AB push, in the session that the HPP was reached, the PROC MIXED model was used with repeated measures of the sow nested within the reward type and a simple correlation structure. Whether PTE (for food or exercise) influenced the HPP and latency to make the first AB push was also explored. The latency variable required square root transformation.

To explore whether there was a relationship between how hard certain sows would work for either reward, Spearman correlation coefficient was calculated for the HPP for different reward types within animals.

To determine how factors may influence the consistency by which pigs focused on pressing the AB, the effects of the reward type, PSE, PTE, BCS, FR and opportunity number on the percentage of AB presses were analysed utilizing a mixed random intercept and slopes model, with the random intercept and slopes of the natural logarithm of FR at the sow level, and random intercept of the opportunity number nested within sow. The random effect of the row number (in which the sow stalls were situated) nested within replicate was added to the model. The percentage of AB presses was converted to the proportion (0.0–1.0, as opposed to 0–100%). The AB proportion required arcsine square root transformation, and the FR scale required a natural log transformation.

3.2.5.2 Behaviour data

To compare the average percentage of time from all opportunities at each FR (calculated from the total duration of time that sows spent in each behaviour), spent in locomotion, exploratory behaviour, snout to snout contact and other behaviours in gilts and sows when out of the stall, the PROC MIXED procedure in SAS with repeated measures of the sow was used. The effects of treatment, type of behaviour and an interactive effect of PSE and type of behaviour were explored. The interactive effect of PSE and type of behaviour was not significant and hence it was removed from the model. The percentages of time, spent in each of the above-mentioned behaviours, were converted to proportion, and then arcsine square root transformed.

To determine whether animals with higher vs lower levels of motivation differed in their behaviour once out of the stall, a separate analysis of each behaviour was performed with the animals split into two populations: a low score population ($n = 14$), animals that reached a maximum FR of 48; and a high score population ($n = 10$), animals that reached a minimum FR of 72. These two populations were analysed in separate models. This approach was taken, as when analysed in a combined model, animals from the low score population had a high number of missing values, due to the absence of data for FR of 72 and above for this population. This led to the higher fit statistics criteria (AICC – Akaike’s information criterion corrected and BIC – Bayesian information criterion) for the combined model than for the separated models.

Mixed models (PROC MIXED procedure in SAS) with repeated measures of the FR and opportunity number and an autoregressive covariance structure were used for the separate analysis of the two populations. Percentages of time spent in locomotion, exploratory behaviour, snout to snout contact and other behaviours were the dependent variables, and all these variables required square root transformation. The effects of the PSE, PTE, BCS, FR, opportunity number, and interaction of the FR and opportunity number were investigated. The non-significant fixed effects were removed from the model. The random effect of the row number nested within replicate was added to the model. For the high score population, the effects of BCS and PTE on the percentage of time spent in locomotion, and the effects of PSE, BCS, PTE and opportunity number on the percentage of time spent in exploratory behaviour, snout to snout contact and other behaviours were not estimated in the initial model containing all the explored effects, and therefore these effects were tested individually one at a time.

3.2.5.3 Control sow data

For the untrained control sows, the mean percentages of AB and DB presses (\pm SEM), and the mean total number of AB and DB presses (\pm SEM) per day presented with the panel, were calculated.

3.3 Results

All animals selected for the current study met the training criteria described in Section 3.2.3.

3.3.1 Motivation

There was a significant interaction between the reward type and PSE for the HPP ($F_{1,44} = 4.23$, $P = 0.046$). Sows showed a significantly greater HPP for feed than movement, but for gilts the HPP for feed and movement did not differ. Sows had a greater motivation to access feed than gilts. Gilts and sows did not differ in their motivation to access movement (Fig. 3.2).

Prior training experience influenced the HPP (for animals, trained for the exercise reward first: 138.17 ± 27.44 vs feed reward first: 225.42 ± 27.44 ; $F_{1,43} = 5.05$, $P = 0.030$), but did not influence the latency to press the AB (Table A.1). Similarly, the latency to press the AB was not influenced by prior stall experience or reward type (Table A.1). Within individual animals, there was a weak positive non-significant correlation between the HPP for feed and movement rewards ($r_s = 0.32$, $P = 0.12$).

The proportion of AB presses was affected by the reward type and the opportunity number. The proportion of AB presses when tested for the movement reward was significantly lower than when tested for the feed reward (exercise reward: 0.76 ± 0.02 , feed reward: 0.86 ± 0.02 ; $F_{1,760} = 40.60$, $P < 0.001$). The proportion of AB presses for the second and third opportunity did not differ, but were higher than for the first opportunity (first opportunity: 0.78 ± 0.02 , second opportunity: 0.82 ± 0.02 , third opportunity: 0.83 ± 0.02 ; $F_{2,732} = 5.84$, $P = 0.003$). There was a tendency for animals trained and tested for the exercise reward first to have a higher proportion of AB presses than animals that were trained and tested for the feed reward first (exercise first: 0.83 ± 0.02 vs feed first: 0.78 ± 0.02 ; $F_{1,18.3} = 3.29$, $P = 0.086$). There were no effects of the PSE (gilts: 0.82 ± 0.03 vs sows: 0.80 ± 0.02 ; $F_{1,17.4} = 0.97$, $P = 0.338$) and BCS (BCS 2: 0.80 ± 0.04 , BCS 3: 0.83 ± 0.02 , BCS 4: 0.80 ± 0.03 ; $F_{2,17.2} = 0.29$, $P = 0.754$), as well as FR (Fig. 3.3) on the proportion of AB presses.

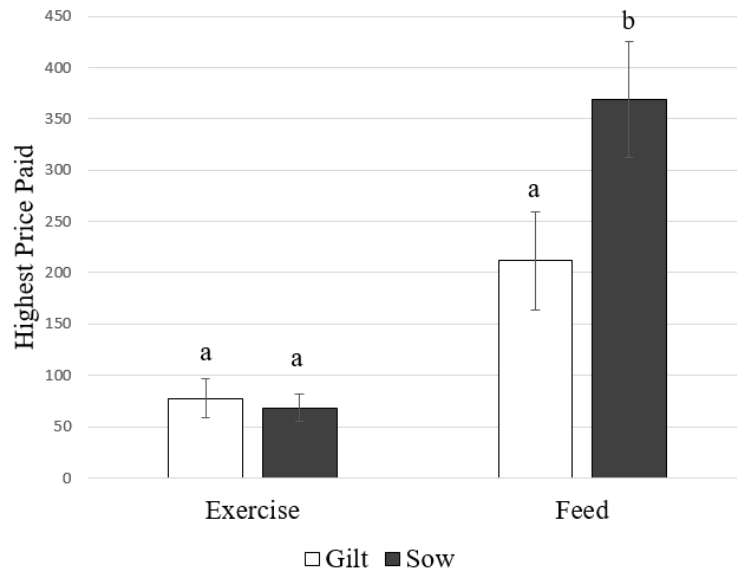


Fig. 3.2. The highest price paid (mean \pm SEM) for gilts (n = 12) or sows (n = 12) to access movement (Exercise), or a feed reward. The non-transformed (raw) mean and SEM values are presented. Where superscripts differ across all values, $P \leq 0.05$.

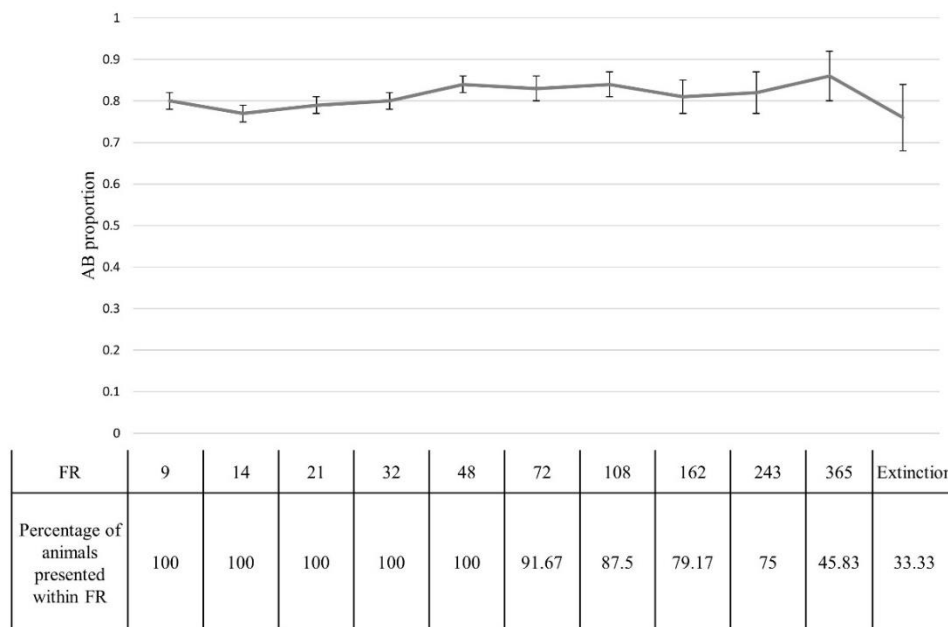


Fig. 3.3. Out of total button presses, the proportion of active button (AB) presses for female swine (n = 24) for different fixed ratios (FR; mean \pm SEM), and the percentage of experimental animals, that were presented within each FR. The non-transformed (raw) mean and SEM values are presented.

3.3.2 Behaviour outside of the stall

3.3.2.1 Comparison of duration of behaviours

There was a significant difference between the proportions of time spent by female pigs in different behaviours ($F_{3,91} = 23.88$; $P < 0.001$). Both gilts and sows spent a significantly higher proportion of time out of the stall in exploratory behaviour than in locomotion and snout to snout contact. Gilts, as well as sows, did not differ in the proportion of time spent in locomotion and snout to snout contact, which was lower than the proportion of time spent by gilts and sows in other behaviours (Fig. 3.4). There was no interaction between PSE and behaviours when out of the stall ($F_{1,91} = 0.15$; $P = 0.703$).

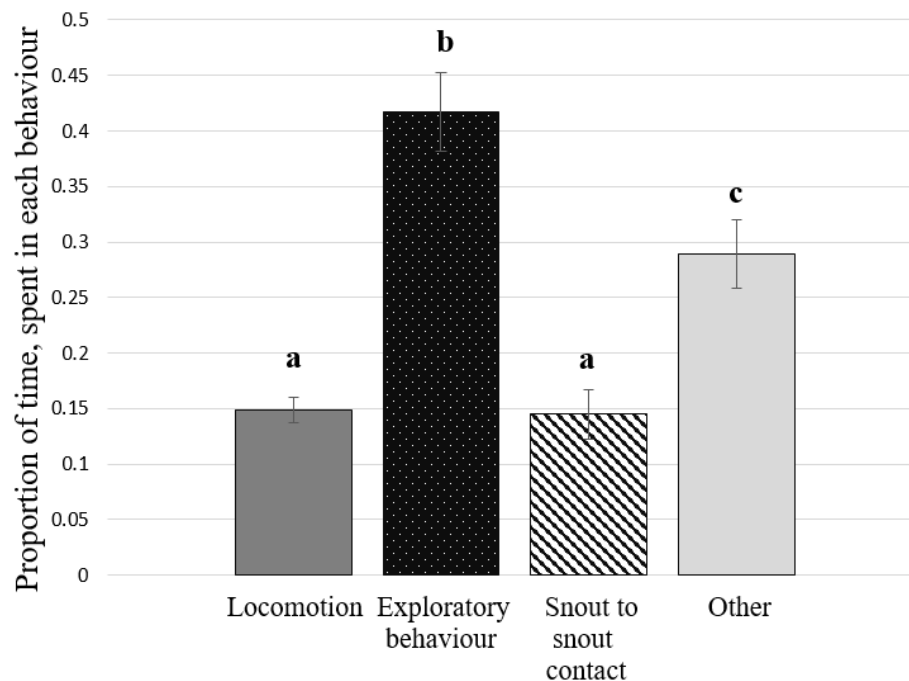


Fig. 3.4. Proportion of time (mean \pm SEM) for female pigs ($n = 24$), spent in locomotion, exploratory behaviour, snout to snout contact and other behaviours. The non-transformed (raw) mean and SEM values are presented. Where superscripts differ, $P \leq 0.05$.

3.3.2.2 Separate analysis of behaviours for high and low score populations

For the high score population (animals that reached a minimum FR of 72), the percentage of time spent in locomotion was influenced by PSE and opportunity number. Once outside of the

stall, gilts from the high score population spent significantly more time in locomotion than sows (gilts: 18.49 ± 1.22 vs sows: 8.58 ± 1.49 ; $F_{1,28.1} = 38.52$, $P < 0.001$). High score animals spent more time in locomotion for their first opportunity to receive a movement reward than for their second and third opportunities, but the percentage of time spent in locomotion for the second and third opportunities did not differ (first opportunity: 16.45 ± 1.14 , second opportunity: 13.49 ± 1.60 , third opportunity: 10.66 ± 1.25 ; $F_{2,34.9} = 13.03$, $P < 0.001$). BCS, PTE (Table A.2) and FR (Table A.3) did not affect the time, spent in locomotion by the high score population.

There was a tendency to spend more time in exploratory behaviour by the animals from the high score population, as the FR increased (FR 9: 38.22 ± 10.12 , FR 14: 44.53 ± 10.15 , FR 21: 44.20 ± 10.12 , FR 32: 52.72 ± 10.15 , FR 48: 50.82 ± 10.19 , FR 72: 53.11 ± 10.44 , FR 108: 65.57 ± 12.84 ; $F_{8,55} = 1.82$, $P = 0.094$). For the FR, the percentages of time spent in each behaviour at FR 162 and 243 were not estimated in the model, hence only the results for FR from 9 to 108 are presented. There was no influence of PSE, BCS, PTE and opportunity number on the percentage of time spent in exploratory behaviour by the high score population (Table A.2). There was no influence of PSE, BCS, PTE, opportunity number (Table A.2) and FR (Table A.3) on the percentage of time spent in snout to snout contact and on the percentage of time spent in behaviours assigned to the category “Other” in the high score population.

In the low score population (animals that reached the maximum FR of 48) there was a significant relationship between BCS and the percentage of time spent in locomotion as well as between the opportunity number and the percentage of time spent on movement (Table 3.2). Animals of BCS 2 had a tendency to spend more time in locomotion than animals of BCS 3, and animals of BCS 2 and BCS 3 spent significantly less time in locomotor behaviour than animals of BCS 4. For the opportunity number, pigs from the low score population spent significantly more time in locomotion for their first opportunity to get a reward of movement, than for the second and third opportunities, but the percentages of time, spent in locomotion did not differ between the second and third opportunities. Also, sows spent more time in locomotion than gilts (Table 3.2). PTE and FR did not influence the percentage of time, spent in locomotion by the low score population (Table A.4).

For the exploratory behaviour in the low score population, the percentage of time spent in exploration tended to be higher for the second opportunity, and was significantly higher for the third opportunity, than for the first opportunity. However, the percentages of time, spent in

exploratory behaviour did not differ for the second and third opportunities (Table 3.2). PSE and BCS (Table 3.2), as well as PTE and FR (Table A.4) did not impact the percentage of time, spent in exploratory behaviour by the low score population.

The percentage of time, spent in snout to snout contact by the low score population, was significantly influenced by PSE and BCS (Table 3.2). Gilts spent more time in snout to snout contact than sows. Animals that had BCS 2 spent less time in snout to snout than animals that had BCS 3, but more time than animals of BCS 4. Animals of BCS 4 also had a lower percentage of time spent in snout to snout contact than animals of BCS 3. There was a tendency to spend less time on snout to snout contact by the low score population for the first opportunity to obtain a movement reward, than for the second opportunity, but the percentages of time spent in snout to snout contact for the first and third opportunities, as well as for the second and third opportunities did not differ (Table 3.2). There was no influence of the PTE and FR on the percentage of time, allotted to snout to snout contact in the low score population (Table A.4).

The percentage of time, spent in other behaviours by the low score population, was not affected by PSE and BCS (Table 3.2), as well as by PTE and FR (Table A.2). However, it was influenced by the opportunity number, with animals spending less time performing these behaviours in the second and third opportunities in comparison to the first opportunity (Table 3.2).

Interactions of the FR and opportunity number were not significant for each behaviour in both high score (Table A.5) and low score populations (Table A.6).

Table 3.2. Percentage of time (mean \pm SEM) spent in locomotion, exploratory behaviour, snout to snout contact and in other behaviours by animals from the low score population (animals that reached the maximum FR of 48; n = 14). The non-transformed (raw) mean and SEM values are presented. Where superscripts differ, $P \leq 0.05$.

Behaviour type	PSE		BCS						Opportunity number					
	Gilt	Sow	F-value	P-value	2	3	4	F-value	P-value	1	2	3	F-value	P-value
	N													
	6	8			2	8	4			14	14	13		
Locomotion	12.15 \pm 3.43 ^a	19.04 \pm 3.14 ^b	4.74	0.040	12.26 \pm 5.11 ^a	7.59 \pm 3.25 ^a	26.92 \pm 3.98 ^b	11.15	< 0.001	18.21 \pm 2.96 ^a	14.68 \pm 3.07 ^b	13.89 \pm 3.09 ^b	4.90	0.015
Exploratory behaviour	31.97 \pm 11.37	51.47 \pm 9.69	1.37	0.254	45.53 \pm 18.06	37.30 \pm 10.45	42.33 \pm 13.45	0.06	0.942	31.48 \pm 4.50 ^a	46.12 \pm 6.67 ^a	51.78 \pm 6.80 ^b	3.44	0.047
Snout to snout contact	29.12 \pm 6.45 ^a	2.80 \pm 5.96 ^b	24.02	< 0.001	19.99 \pm 9.09 ^a	36.05 \pm 6.10 ^b	8.17 \pm 7.35 ^c	16.37	< 0.001	11.81 \pm 5.55	18.56 \pm 5.88	17.51 \pm 6.40	2.91	0.071
Other	23.65 \pm 11.48	24.79 \pm 10.44	0.10	0.752	14.60 \pm 17.33	15.04 \pm 11.00	43.01 \pm 13.38	1.67	0.216	39.44 \pm 10.14 ^a	21.63 \pm 10.17 ^b	11.59 \pm 10.63 ^b	7.76	0.003

Abbreviations: PSE, prior stall experience; BCS, body condition score

3.3.3 Control sows

Additional control sows ($n = 8$) that were presented with the operant panel for 30 minutes on each of six consecutive days and initially interacted with the panel, maintained similar levels of interaction with the operant panel (Fig. 3.5) over the course of six days, with the average of $50.20 \pm 33.74\%$ (mean \pm SD) of AB presses, and $49.80 \pm 33.74\%$ (mean \pm SD) of DB presses for the whole course of the panel presentation, with high individual variation.

The control sows were generating total push button counts on day 1 within the range of the HPP reached by sows and gilts for access to time out of the stall. However, over the course of the six-day presentation, the total interaction with the panel reduced (day 1: 139.88 ± 92.69 vs day 6: 52.25 ± 105.41 , mean total number of button presses \pm SD).

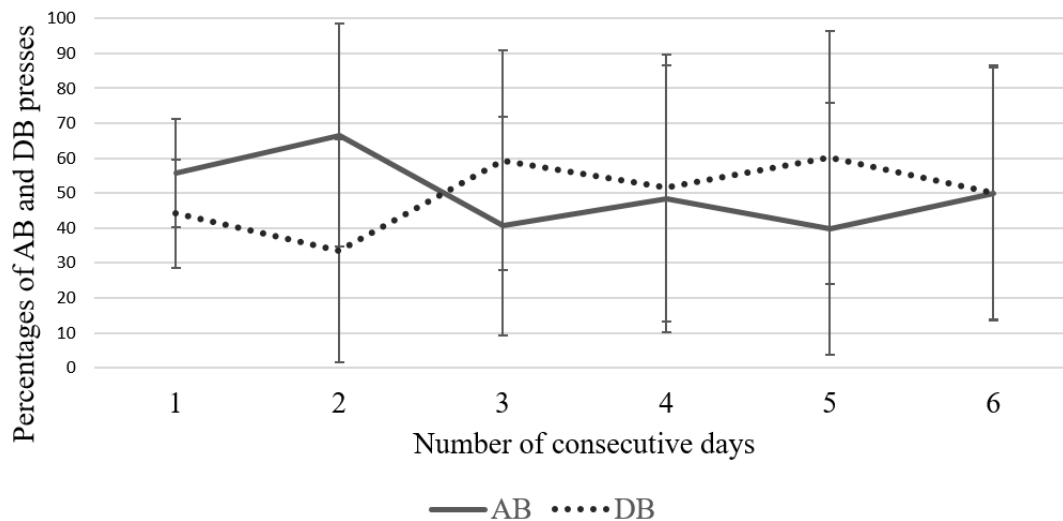


Fig. 3.5. Percentage of the active button (AB) and dummy button (DB) presses, made by untrained control sows ($n = 8$) when presented with the operant panel for 30 mins/day for six consecutive days (mean \pm SD).

3.4 Discussion

The aim of the present study was to determine the motivation of gestating stall-housed sows and gilts to exit the stall for a greater freedom of movement and to understand more about the strength of this motivation by comparing it to their motivation to work for a resource of high value, food.

In control sows, which were not rewarded, total levels of interaction with the operant panel were surprisingly high. This can be explained by different factors: first, the control sow data were presented as a total of AB and DB presses, whereas for the experimental animals only the AB push counts were analysed. Second, the control sow results describe a level of interaction with the panel during 30 mins of the panel presentation, whereas for the experimental animals only the results for one opportunity to get a reward are presented, which in most cases took less than three minutes. Third, such intensive interaction with the panel in untrained sows may indicate the exploratory drive which is particularly high in pigs. Manipulable enrichment is important for pigs, providing an outlet for the expression of innate behaviours (Tuytens, 2005). The importance of environmental enrichment was also demonstrated by Elmore et al. (2012), who found a significant level of motivation to access compost and straw by sows, as indicated by operant responding. Interestingly, levels of interaction with the operant panel in the control sows towards the end of the trial were similar to the average levels of interaction with the operant panel to access an empty trough, reported by Elmore et al. (2012), which supports the theory about the role of the panel in enriching the barren stall environment. Nevertheless, it was observed that over the course of the six-day presentation, the total interaction with the panel in control sows declined. By contrast, the experimental sows that had been trained to associate interaction with the panel with receiving a reward maintained levels of interaction with the panel over consecutive days and as the FR increased, providing further evidence that experimental animals understood that continued pressing of the panel would result in a reward.

Both gilts and sows had a certain level of motivation to leave the stall, which indicates the presence of a need for freedom of movement in stall-housed gestating female pigs. As hypothesised, the motivation for food was higher than the motivation for movement (as indicated by the HPP), but only in sows. This outcome is in agreement with the results of Elmore et al. (2012) and can be explained by the fact that food is a resource of known high value (Patterson-Kane et al., 2011). However, gilts expressed similar levels of motivation for greater freedom of movement and food, which suggests that these resources are equally valued by gilts. This is further supported by the fact that all the experimental animals showed a high level of precision pressing the AB, as discussed in Section 3.3.1, therefore it is not likely that gilts were less trained, or more distracted than sows when using the panel. Sows and gilts did not differ in their level of motivation for exercise, which implies that motivation for movement in female pigs does

not depend on their PSE. These findings are in agreement with the behavioural results which demonstrated that sows and gilts did not differ in the proportions of time spent in locomotion when being out of the stall. The greater motivation for feed in sows may be due to the fact that sows were recovering from lactation at the time of testing, or due to larger body size and hence higher energy deficit in feed-restricted sows in comparison to smaller gilts.

The latency to press the AB was recorded as a further measure of motivation, representing the eagerness of the pig to interact with the panel and start working towards the required FR. Unlike in the study of Elmore et al. (2012), the latency to make the first AB push was not affected by the reward type. The experimental design of the current study was different from that described by Elmore et al. (2012). The operant panel in the present study contained two buttons, and only the latency to make the first AB push was recorded, whereas in some situations the pigs could press the DB first. In contrast, Elmore et al. (2012) recorded the latency to push a single panel button. The importance of this measure might also be questionable, as the study of Elmore et al. (2012) showed that the HPP was significantly higher for food than for other resources (compost and straw), but the latency to press the operant panel for all three recourses did not differ. Similarly, in the current study the latency results could imply that the animals are equally motivated to access both rewards, but this was not confirmed by the HPP results. This measure may also not be as valid, as the pigs could be eager to interact with the panel due to their strong motivation to explore.

A higher motivation to obtain a reward in animals trained and tested for a feed reward first provides further evidence that female pigs value this reward more, which is in agreement with the results of Paterson-Kane et al. (2011) and Elmore et al. (2012). The presence of motivation in both groups with different PTE confirms that pigs are trainable to interact with the panel for different types of reward, as previously shown by Kirkden and Pajor (2006b) and Elmore et al. (2012). But more importantly, these results show that pigs can be retrained to interact with the panel for different resources, which has not been presented in the previous studies. This is further supported by the fact that the percentage of AB presses of trained animals was high, in comparison to the high variability in button presses by control sows.

The operant panel was designed with two buttons specifically to measure the precision at which sows selected the AB. A higher proportion of AB presses when pigs worked for food than for movement implies that pigs are working more precisely for the resource that they value more.

It is also important to take into account the relationship between the proportion of AB presses and the opportunity number. An increase in precision of interaction with the panel within one testing session is an indicator of sow learning ability and may suggest a better use of short-term memory in operant tasks. But it may also suggest that sows are working more precisely when they are more habituated to the panel, which works as an element of environmental enrichment, and this habituation develops quickly, as the percentages of AB presses for the second and third opportunities did not differ.

Comparing the proportion of time spent by sows and gilts in each behaviour when out of the stall highlights the importance of exploratory behaviour in the behavioural repertoire of the pig. That gilts and sows spent equal proportions of time in locomotion when out of the stall is in agreement with the results of the HPP, that they were equally motivated to access time out of the stall. That the proportion of time spent in movement and in social interaction were equal between both PSE groups, suggests that female pigs have basic needs for exercise and for social contact, which are not dependent on their previous stall experience. These results are in agreement with the findings of Matthews and Ladewig (1994), who discovered that pigs are motivated to access social contact when working on an ascending FR schedule, but the elasticity of demand for social contact was higher than for a feed reward. In another study, Hemsworth et al. (2011) found that 15-20 week old female pigs in a Y maze choice test consistently preferred social contact over bedding, which confirms that pigs value having access to social contact. The authors also reported that gilts chose social contact over feed in another Y maze choice test, with high individual variation, which could be related to the difference in the deprivation levels in this test: the tested animals were highly deprived of social contact with the elimination of both tactile and visual contact, but food deprivation was more moderate with gilts receiving 70% of their ad-libitum feed intake. Considering the fact that pigs are very social animals and in natural conditions sows usually live in small groups (Rhodes et al., 2005), it can be argued that social contact is as important as greater freedom of movement, and should be considered when developing methods to improve the welfare of stall-housed sows.

The separate analysis of behaviours according to high and low score populations revealed that gilts from the high score population with a higher motivation to access a greater freedom of movement were more driven by a desire to exercise, than sows, which was not observed in the low score population.

Within each testing session, animals had three opportunities to access the reward. Animals from both high and low score populations showed that their desire to move decreased within one testing session, with the greatest amount of locomotion occurring during the first opportunity to exit the stall. The increased performance of a certain behaviour after a period of deprivation with a following decrease of performance is an indicator of a rebound effect, which, according to Dawkins (1988), indicates the presence of strong motivation. On the other hand, this finding also suggests that if exercised daily, the required levels of exercise for gestating female pigs could be rather low (especially considering that the levels of locomotion for the second and third opportunity did not differ in both the high score and low score populations). This is in agreement with the study of Rioja-Lang et al. (2013), which found that when giving sows the option to remain in the stall or to access a group area, they would spend over 82% of their time budget in the stall. The nutritional status, social status and environmental complexity should also be taken into account, for each of these factors are believed to strongly influence sow motivation (Rhodes et al. 2005). The animals had a stronger motivation to explore the environment when out of the stall, confirming that the ability of the animals to perform exploratory and foraging behaviours may be more important than exercise.

At the same time, the animals were presented with the operant panel daily and chose to leave the stall every day when given an opportunity. These results may indicate the need for access to a greater freedom of movement on a daily basis. Moreover, this may indicate the intrinsic need for pigs to have opportunities for control over their environment, which cannot be achieved in stall-housing (Rhodes et al., 2005). When considering the Code of Practice (NFACC, 2014) requirement to provide a greater freedom of movement to stall-housed gestating female pigs, having the opportunity to exercise should not be the only consideration for improving animal welfare. A more complex approach, which includes elements of giving sows control over their environment, as well as providing social interaction and exploratory and foraging opportunities, should be taken.

The existing relationship between the BCS and time spent in locomotion when outside of the stall for the low score population suggests that over-conditioned sows are moving more, than thinner animals. This may be due to over-conditioned sows having a lower motivation for exploration compared to thinner sows.

The percentage of time spent in exploratory behaviour tended to increase over the days on trial in the high score population, and within one testing session in the low score population. This is also an indicator of sow learning and cognitive abilities and may suggest that animals asked for time outside of their stalls due to memories that on the previous day, or when receiving their previous movement reward, there possibly was an opportunity to find some additional food outside of the stall. Due to this factor, they could increase their panel interaction performance and also become more feed-search and hence exploration oriented when being outside of the stall, over the course of time. However, prior to the start of each testing day, the alleyway floor between the stalls was swept clean, preventing or reducing the loose feed animals could obtain. Therefore, we propose that this result is observed because a predominant behaviour of pigs is feed seeking, so they are returning to their typical behaviour repertoire when given the opportunity (Stolba and Wood-Gush, 1989). On a larger scale, these results highlight the dominant role of hunger in shaping the behaviour of feed-restricted sows, as feed restriction increases foraging motivation, the performance of oral behaviours and restlessness in sows (Appleby and Lawrence, 1987; D'Eath et al., 2018). Hence, in order to improve sow psychological well-being, this factor should necessarily be addressed, especially considering the fact that modern pregnant sows are fed less than half (44.1%) of their ad libitum feed intake (Read et al., 2020). Additionally, given that the percentage of time spent in snout to snout contact in the high score population numerically decreased over the course of testing while the percentage of time spent in exploratory behaviour was increasing, it can be argued that deprivation from social contact can also produce a rebound effect, which indicates the presence of the behavioural need for social interaction in sows.

The results of the proportion of time spent in snout to snout contact in the low score population suggest that gilts have a higher need to maintain social contact than sows, maybe due to higher levels of curiosity and exploratory behaviour, present in younger animals to maintain the learning process. However, these results are applicable only for the population with lower levels of motivation to access time outside of the stall. In the same population, animals with an ideal BCS were the most social, with thin animals having an intermediate level of snout to snout contact, and over-conditioned animals having the lowest scores. This could be due to the difference in the social rank between animals having different BCS, with dominant sows being heavier than subordinate sows (Hoy et al., 2009). Given that a hierarchy in the group of sows is

maintained by subordinate animals actively avoiding dominant rather than by dominant sows attacking subordinate sows (Gonyou, 2001), it can be assumed that the sows with higher BCS in the current study were more socially passive due to being dominant. Another possible explanation is that excessively over-conditioned animals may have a lower desire to interact with conspecifics, maybe because of reduced locomotor capabilities, required for social interaction. Lower desire to interact with other sows in the group of animals with BCS 2 in comparison to the sows with BCS 3 can be explained by a higher motivation to receive additional feed than to establish social contact in thin animals.

The percentage of AB presses made by trained experimental sows was consistently high, being in a range of 79–89%. In comparison, for the control sows the average percentage of interaction with both the active and dummy buttons was similar. This confirms that the experimental sows were interacting with the AB not due to individual preferences to press this button, but because they were trained to associate the AB interaction with obtaining a reward. This conclusion is supported by the study of Matthews and Ladewig (1994), who found that pigs trained to associate the reward with responding on the operative plate had a very low number of responses on the alternate inoperative plate under all testing conditions.

3.5 Conclusions

Sows that were previously stalled and gilts who have not experienced stalls value access to a greater freedom of movement, as determined by the HPP. However, the prior stall experience influences motivation to access different rewards in animals: sows have a moderate level of motivation in comparison to the motivation for feed, whereas for gilts, the motivation to work for time out of the stall is as strong as the motivation to work for feed. In contrast, the higher proportion of AB presses for the feed reward than for the movement reward suggests that motivation to leave the stall is moderate in comparison to the motivation for feed in both gilts and sows. Analysis of behaviour when outside of the stall confirms that animals have a level of motivation to exercise, but having an opportunity for exploration is an important part of the motivation to get out of the stall and likely relates to the fact that gestating sows are feed restricted and they maintain a strong innate exploratory drive. Now, when the presence of sow motivation for movement is confirmed, it is important to clarify the welfare and production benefits of providing a greater freedom of movement. The findings of this study have

implications for understanding animal needs and acceptability of animal housing and management to provide for their needs.

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4. THE INFLUENCE OF SATIETY ON THE MOTIVATION OF STALL-HOUSED GESTATING SOWS TO EXIT THEIR STALL

The results of the study described in Chapter 3 indicated the presence of the motivation in gestating female pigs to leave the stall. However, it was also found that for sows the motivation to exit the stall was lower than that for food, and when being outside of the stall, sows spent most of their time in exploratory behaviour and a lower proportion of time in locomotion. These findings suggest that opportunities for exploration when outside of the stall may be more valued by the sow than having access to exercise per se, which needs to be explored further. In Chapter 4, the motivation to leave the stall in sows kept at different levels of satiety was studied. The results demonstrate that the strength of motivation to leave the stall is influenced by satiety. The behavioural results are in agreement with those presented in Chapter 3, and suggest the presence of an intrinsic need for exploration in stall-housed gestating sows, as satiated sows continued to work for time out of their stalls.

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Abstract

The welfare of stall-housed gestating sows is a point of public concern worldwide. In Canada, the Code of Practice for the Care and Handling of Pigs (2014) proposed allowing the operation of existing stall barns after 2024, if bred female pigs are given opportunities for greater freedom of movement. The objective of this study was to explore whether the motivation of stall-housed gestating sows ($n = 42$) to leave their stall is influenced by satiety. Sows were assigned to one of three treatments: control (C), fed a standard ration (2.3 kg of feed/sow) only; moderately satiated (0.5 HF), standard ration and 50% of their ad-lib high fibre (HF) intake; fully satiated (ad-lib HF), standard ration and unlimited access to HF. Sows were trained to use an operant panel containing two buttons: i) active button (AB – push counts resulted in a reward of movement), ii) dummy button (push counts not rewarded). The required number of AB presses during a testing session increased by 50% each day. Animal behaviour once out of the stall was continuously video recorded. Control sows showed a greater highest price paid (HPP, maximum AB push counts in one session) than ad-lib HF sows, with 0.5 HF sows being intermediate (C: 94.43 ± 18.21 , 0.5 HF: 66.43 ± 5.88 , ad-lib HF: 59.14 ± 23.65 ; $F_{2,39} = 3.38$, $P = 0.044$, mean HPP \pm SEM). When out of the stall, sows from all treatments spent the greatest proportion of time in exploratory behaviour (Ex). The proportion of time spent in snout to snout contact (S) was significantly lower than the amount of time spent in other behaviours (O), with the proportion of time spent in locomotion (L) being equal to the amount of time spent in snout to snout contact and in other behaviours (L: 0.15 ± 0.01 , Ex: 0.52 ± 0.03 , S: 0.12 ± 0.01 , O: 0.20 ± 0.02 ; $F_{3,156} = 74.30$, $P < 0.001$, mean proportion of time \pm SEM). Results suggest that stall-housed sows are motivated to exit their stalls, and the strength of motivation is influenced by satiety. Behavioural results indicate the presence of an intrinsic need to perform exploratory behaviour, supported by the fact that satiated sows continued to work for time out of their stalls.

Keywords: Pig, Operant conditioning, Gestation stalls, Exercise, Welfare, High fibre.

4.1 Introduction

The welfare of pregnant sows housed in gestation stalls is a subject of public debate around the world. The societal expectation is that gestating sows will be provided with opportunities for a greater freedom of movement, such as keeping sows in group housing, reducing the physical and social restrictions experienced by stalled animals (Tonsor et al., 2009; Elmore et al., 2012;

Spoolder and Vermeer, 2015). Multiple countries (including the EU, New Zealand and Australia) have banned stall housing systems (CEC, 2008; NAWAC, 2010; Primary Industries Standing Committee, 2008).

In Canada, the Code of Practice for the Care and Handling of Pigs (NFACC, 2014) requires all new barns to house bred sows and gilts in groups. However, the Code of Practice includes a grandfather clause to permit the housing of gestating sows in existing stall barns built prior to 2014, given that as of 2024, these animals are provided with the opportunity for greater freedom of movement.

One of the viable methods to provide a greater freedom of movement to sows is to release sows from stalls individually to periodically exercise in the alleyways. Previous studies suggest that providing periodic exercise through intensive regimes positively affects the sows' musculo-skeletal system by enhancing bone strength, periodic exercise also increases umbilical blood flow and appears to reduce restlessness of sows (Schenck et al., 2008; Harris et al., 2013).

However, the core concept of welfare involves not only the animal's physical health but also its mental health, including innate desires and feelings (Dawkins, 2003; Kirkden and Pajor, 2006). If providing periodic exercise to gestating sows is going to be proposed, it needs to be understood how sows value time out of their stalls. One scientific method for determining how animals value different aspects of their environment is to use motivation tests. This approach was previously used to evaluate the motivation of stall-housed gestating pigs to access time out of their stall, as discussed in Chapter 3. This previous study indicated that stall-housed sows and gilts are motivated to leave their stalls; with gilts being equally motivated to exit the stall and to access food, whereas for sows the motivation to exit the stall was less than that for food. It was also found that when outside of the stall, sows spent most of their time in exploratory behaviour and a lower proportion of time in locomotion. This suggests that sows asked to exit their stall primarily for exploration and hence having an opportunity to exercise per se may not be as important for sows and rather, having opportunities to perform motivated behaviours may be more valued.

In commercial conditions gestating sows are feed-restricted to as low as 50% (Whittemore et al., 1977) or even 44.1% (Read et al., 2020) of their ad-lib intake in order to prevent excessive weight gain (Ramonet et al., 1999; Meunier-Salaun et al., 2001; de Leeuw and Ekkel, 2004). These feed restrictions help to maintain healthy weight and production but do not allow sows to

satisfy their hunger (Read et al., 2020). Consequently, stall-housed gestating sows may be motivated to exit the stall to acquire more feed. Supplementing the sow gestation ration with high fibre can provide gut fill, increasing satiety while maintaining the desired energy intake levels (Holt et al., 2006; D'Eath et al., 2018; Jarrett and Ashworth, 2018).

The objectives of this study were to determine whether and how the motivation of gestating sows to leave their stall changes when fed diets, which resulted in sows being hungry (standard gestation diet and no high fibre feed), moderately satiated, or fully satiated, and to explore whether the behaviour of sows when out of the stall differed per treatment. The motivation of sows was evaluated by measuring the animal's willingness to interact with an operant panel for a reward of three minutes of time out of the stall and comparing it across the different dietary treatments. Additionally, whether the sow worked harder to exit the stall influenced her behaviour when out of the stall was explored through the comparison of sows which demonstrated lower levels of interaction with the operant panel and sows having high levels of interaction with the operant panel.

4.2 Materials and methods

All experimental procedures were approved by the University of Saskatchewan Animal Care Committee (#20170057), which is regulated by the Canadian Council of Animal Care (2009). This experiment was conducted daily between June and August of 2018 at the Prairie Swine Centre, Saskatoon, Canada.

4.2.1 Animals and husbandry

A total of 42, Camborough 42 sows (parities 2-5, 2.98 ± 0.91 parities, mean \pm standard deviation [SD]) were studied. The animals were trained to interact with an operant panel to obtain a reward of three minutes of time out of their stall. All animals were bred and kept in stalls (2.1 m x 0.62-0.73 m) with part-slatted flooring and remained on trial until they completed their own testing schedule. To work in line with the barn production flow, the animals were selected at 7-10 days post breeding. A total of six experimental sows were selected within one breeding week, forming one replicate block, with a total of seven replicate blocks. Body condition score (BCS) was determined and recorded for each experimental sow on the first day of the operant panel training. The distribution of sows according to their BCS was as follows:

BCS 2: n = 4; BCS 3: n = 31; BCS 4: n = 7. Sows were fed 2.3 kg of a standard gestation pelleted ration containing 2.25 Mcal/kg, 11.96% crude protein and 4.55% crude fibre once a day at 07:00 h, and this feeding regime was kept constant during the study. Each individual stall was equipped with a nipple drinker.

4.2.2 Treatments

Sows were assigned to one of three treatments (two sows per treatment in each replicate, n = 42 sows, 14 per treatment): 1: Sows fed only their standard gestation ration, with no additional feed (control: C); 2: Sows receiving 50% of their ad-lib amount of high fibre (HF) feed once per day additional to their standard ration, one hour prior to the beginning of a testing session (0.5 HF); and 3: Sows given an opportunity to consume high fibre feed ad libitum, in addition to their standard ration, starting one hour prior to the beginning of the testing session and up to the beginning of their testing (ad-lib HF). To achieve different levels of satiety a high fibre feed was chosen, as sow satiety is largely influenced by gut fill, which can be effectively increased by consumption of fibrous feed (Jarrett and Ashworth, 2018). Preliminary studies identified that timothy hay cubes were a preferred source of high fibre feed for gestating stall-housed sows, in comparison to beet pulp and chopped hay. Timothy Cubes (Ontario Dehy, Goderich, Ontario, Canada) soaked overnight in hot tap water (1:2 timothy cubes to water volume ratio) served as a source of high fibre, which was fed after their standard concentrate ration. The timothy cubes contained 8% crude protein (min), 38% crude fibre (max) and 2% crude fat (min). The sows remained on the same dietary treatment throughout the experiment.

Based on the results of preliminary trials, a strategy for determining the individual ad-lib amount of high fibre feed was developed. Three days prior to the beginning of the operant training, the ad-lib high fibre feed consumption levels were determined for each sow assigned to the 0.5HF and ad-lib HF treatments: during three days the sows received access to an ad-lib amount of high fibre feed. The amount of feed consumed in one, two and three hours after the feed was given was recorded by weighing the feed left in a trough at each of these time points. Great variability in the speed of consuming the high fibre feed was observed. Based on these data, an average ad-lib high fibre feed consumption at each of the above-mentioned time points for each sow was calculated.

To prevent sows developing an association between interaction with the panel and receiving high fibre feed, during the period of operant training sows from all three treatments were fed only their standard gestation ration with no addition of high fibre. During the testing period, the sows from 0.5 HF and ad-lib HF treatments were given 50% and 100% of their ad-lib high fibre feed intake, accordingly. The amount of feed for each sow depended on the planned time of her testing (testing order). E.g. a sow from the 0.5 HF treatment, which was to be tested two hours after getting access to high fibre feed, received 50% of her average ad-lib feed consumption within a two hour period. Sows were presented with high fibre feed right after they finished their standard ration meal. Prior to the start of testing, ad-lib HF sows always had feed remaining in their trough and had ceased eating, indicating they were satiated. The remaining food was removed from the trough right before the operant panel was attached to the stall gate to ensure the sow focused on the panel and did not interact with food in the trough. Sows from 0.5 HF treatment were observed to consistently consume all their HF ration before the start of testing, hence no feed was removed from their troughs.

4.2.3 Experimental apparatus

For the detailed description of the experimental apparatus refer to Chapter 3. An operant panel (refer to Fig. 3.1 for photograph), with two identical buttons and a central divider between them, was used to measure sow motivation. One button was designated as the active button (AB), and push counts to this button resulted in an exercise reward for the animal. The other button was designated as the dummy button (DB) and acted as a control measure. Two LED lights flashed when the required number of button presses was reached. One of the lights was positioned above the buttons of the panel, and another one was visible to the researchers on the control box, containing the microcomputer. The operant panel was hung inside the front gate of the stall. The number of AB push counts required to receive a reward was preprogrammed into the microcomputer, and both numbers of AB and DB push counts were recorded.

4.2.4 Experimental procedure

Sows were given their daily gestation feed ration in the stalls at 07:00 h each morning in accordance with farm practice and were allowed one hour to consume their meal. Training and testing of all sows on trial took place from 08:00 h to 14:00 h each day. The order of training and

testing of individual sows within each replicate was randomised each day. Each sow received access to the operant panel for a total of 30 minutes per training/testing session and was trained to press one of the buttons to receive a reward of time out of the stall. The buttons designated as AB and DB were switched per replicate.

Prior to testing, all sows were trained over the course of three days to press the AB on a gradually increasing training schedule from one button press up to a total of nine times, with three consecutive opportunities within each training session. For additional details on the training procedures used in this study, refer to Chapter 3. Sows that failed to meet the training criteria by day three were given up to two additional days to meet the criteria. After the initial training, sows moved on to testing. For reaching the assigned fixed ratio (FR) by pressing the AB, sows were rewarded with an opportunity to freely move around within the alleyway between stalls for three minutes. To receive this reward, the sows were let out of the stall. For this, the human handler opened the stall gate fully, and stood out of the way, and out of view of the sow exiting the stall. The sow was left to exit the stall by herself. There was no human-animal interaction. The alleyway was swept clean before the beginning of testing to remove any spills of feed. When being in the alleyway, experimental sows had access to social interaction with other animals through the bars of their stall gates. For training, a small amount of jam was applied to the AB to attract the sows' attention to it.

Once trained, sows were tested on an ascending FR schedule, with the required number of AB button presses increasing by 50% each day from a FR 9, up to a maximum FR 365, which produced a testing schedule of FR 9, 14, 21, 32, 48, 72, 108, 162, 243, 365.

Each sow was given 30 minutes and a maximum of three consecutive opportunities to reach the required FR and obtain the reward. If the sow failed to reach the required FR, no reward was given and the sow received a second opportunity to reach the required FR the following day. Should the sow fail to reach the required FR for a second day, testing ended and the sow was off trial. Any sow that met the FR of 365 was presented with the panel for one additional day and the maximum number of AB presses the sow made within a 30-minute period was recorded (extinction day).

The highest price paid (HPP) was defined as the maximum AB push count achieved by a sow over the whole period of testing, and it was recorded for every sow as an indicator of sow motivation for the resource. As an additional measure of motivational strength, the latency to

make the first AB push in the session when the HPP was reached was recorded (Elmore et al., 2012). The percentage of AB presses was calculated and analysed as an additional measure of motivation and sow learning abilities, as well as the intensity with which sows interacted with the panel.

4.2.5 Behavioural observations

Once out of the stall, the behaviour of sows was continuously recorded with a video camera, the Sony HDR-CX405 (Sony Corp., New York, NY, USA), mounted on the wall at the end of the alleyway into which sows exited the stall (Table 4.1). The durations of each sow behaviour during testing for motivation to exit the stall were calculated. For the final analysis, the total duration of time (s) spent in exploratory behaviour, snout to snout contact, locomotor behaviour (total of durations of walking, trotting and running/scamper) and other behaviours (the total of durations of licking bars, defecating, urinating and time out of sight) were used.

Similar to Goumon and Spinka (2016), a 15% sample of all videos was rewatched by the same observer for intra-rater reliability. The following intraclass correlation coefficients (ICC) were obtained: 0.945 for locomotor behaviour, 0.972 for exploratory behaviour, 0.950 for snout to snout contact and 0.973 for other behaviours. Results with $ICC > 0.9$ are considered as excellent (Koo and Li, 2016).

Table 4.1. Behavioural descriptions for assessing sow activity outside the stall.

Category	Behaviour	Description
Locomotion	Walking	The animal is moving at a slow pace and always has two or three feet on the ground at any one time.
	Trotting	The animal is moving at a quick pace, between a walk and a run, in which legs move in diagonal pairs in a two-beat diagonal gait.
	Running/scamper	The animal is moving at a pace faster than walking and trotting. Running is represented by a controlled three-beat gait. Scamper includes hopping with both hind legs moving in unison.
Social	Snout to snout contact	The animal has a snout to snout contact with another sow through the gate of the stall.
Exploration/ foraging	Exploratory behaviour	The animal is exploring the environment (travelling forward or backwards with a snout on the ground, either in the centre of the alley or along the stalls. The sow may be standing, or kneeling and/or trying to place head under the bottom bar of the stall gate and reach feed inside the stall); eating if feed was reached.
Other	Licking bars	The animal is licking bars of the gate of an empty stall.
	Defecating	The animal is releasing faeces on the ground while moving or standing still.
	Urinating	The animal is releasing urine on the ground, usually while standing still.
	Out of sight	The animal cannot be seen.

4.2.6 Statistical analysis

Data were analysed with the statistical package SAS 9.4 (SAS Institute, Cary, NC, USA). The significance level was set at $P < 0.05$. Results with $P < 0.10$ were considered as statistical trends. Post model analysis of residuals of all dependent variables was examined for normal distribution using PROC UNIVARIATE, considering the Shapiro-Wilk test for normality and a normal probability plot, and the data were transformed as necessary. The fit statistics of models were also checked through the Akaike's information criterion corrected (AICC) and Bayesian information criterion (BIC) to ensure the best fit model was achieved, and residuals of all final models were examined for normality and homogeneity of variance. For all model output, the least square means (LSMEANS) of fixed effects with Tukey adjustment was used to account for multiple comparisons. Results are presented in the mean and SEM from the raw (not transformed) data as computed from the final model.

4.2.6.1 Motivation measures

To determine the influence of treatment on the HPP (maximum AB push counts over the whole testing session) and latency to make the first AB push, in the session that the HPP was reached, the PROC MIXED model with the random effect of parity was used. The independent effects of BCS and treatment were included, however the BCS variable was non-significant in both of the models and was removed from the final models. HPP and latency variables required log base 10 transformation.

The effects of treatment, BCS, parity, FR and opportunity number on the percentage of AB presses for each FR and opportunity reached by each sow were analysed utilizing a mixed random intercept and slopes model, with the random intercept and slopes of the natural logarithm of FR at sow level, and random intercept of the opportunity number nested within sow. The FR, opportunity number and BCS were removed from the final model as non-significant independent variables, whereas parity (due to its biological significance) and treatment were kept in the final model. The percentage of AB presses was converted to proportion.

4.2.6.2 Behaviour when out of the stall

To compare treatment effects on the behaviour of sows when out of the stall, the average percentage of time (combined from all opportunities at each FR and calculated from the total

duration of time that sows spent in each behaviour), which sows spent in locomotion, exploratory behaviour, snout to snout contact and other behaviours when out of the stall, was compared using the PROC MIXED procedure with repeated measures of the sow in SAS. The effects of treatment, type of behaviour and an interactive effect of treatment and type of behaviour were explored. The interactive effect of treatment and type of behaviour was not significant and hence it was removed from the model. The percentage of time, spent in each of the above-mentioned behaviours, was converted to a proportion, and then arcsine square-root transformed.

To determine whether how hard sows worked for time out of the stall influenced their behaviour when out of the stall, the sows were divided into two populations: a low score population ($n = 27$), of sows that reached a maximum FR of 48; and a high score population ($n = 15$), of sows that reached a minimum FR of 72. The low score population was represented by sows from all three treatments: control ($n = 7$), 0.5 HF ($n = 9$) and ad-lib HF ($n = 11$). The distribution of sows from different treatments in the high score population was as follows: control ($n = 7$), 0.5 HF ($n = 5$), ad-lib HF ($n = 3$). The two populations were analysed in separate models. This approach was taken, as when analysed in a combined model, sows from the low score population had a high number of missing values, due to the absence of data starting from the FR of 72 for this population. This led to the higher fit statistics criteria for the combined model than for the separated models.

A mixed model (PROC MIXED procedure in SAS) with repeated measures of the FR and the opportunity number within sow and an autoregressive covariance structure was used for the separate analysis of the two populations. The percentage of time spent in locomotion, exploratory behaviour, snout to snout contact and other behaviours were the dependent variables and all required square root transformation. The effects of treatment, parity, BCS, FR, opportunity number and interaction of the FR and opportunity number were investigated. Interactions of the FR and opportunity number were not significant for each behaviour in both high score and low score populations and hence were removed from all the final models.

4.3 Results

All sows, selected for the current study met the training criteria described in Section 4.2.4. The results are presented as the mean \pm standard error of the mean (SEM). For the main effects,

P-values and F-values are presented, and adjusted P-values are presented for post hoc comparisons.

4.3.1 Motivation to exit the stall

There was an effect of treatment on the HPP ($F_{2,39} = 3.38$; $P = 0.044$). Control sows showed a greater HPP than sows fed ad-lib HF, with sows fed 0.5 HF being intermediate (Fig. 4.1).

The latency to press the AB was not influenced by sow treatment (C: 6.51 ± 12.66 , 0.5 HF: 14.33 ± 12.84 , ad-lib HF: 15.08 ± 14.74 ; $F_{2,35} = 0.04$, $P = 0.965$).

The proportion of AB presses was not affected by treatment (C: 0.81 ± 0.03 , 0.5 HF: 0.78 ± 0.04 , ad-lib HF: 0.78 ± 0.04 ; $F_{2,22.3} = 0.45$, $P = 0.646$) or by parity (parity 2: 0.79 ± 0.03 , parity 3: 0.82 ± 0.03 , parity 4: 0.78 ± 0.04 , parity 5: 0.78 ± 0.08 ; $F_{3,29} = 0.45$, $P = 0.781$).

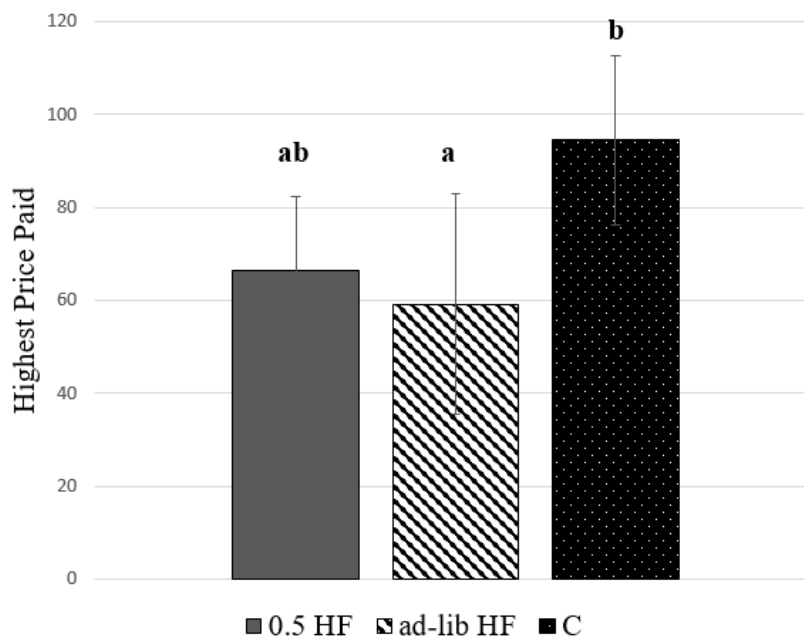


Fig. 4.1. The highest price paid (mean \pm SEM) for sows receiving 50% of their ad-lib high fibre feed intake (0.5 HF, $n = 14$), fed high fibre feed ad-lib (ad-lib HF, $n = 14$) and control sows receiving no high fibre feed additional to their standard ration ($n = 14$) to access movement. The non-transformed (raw) mean and SEM values are presented. Where superscripts differ, $P < 0.05$.

4.3.2 Behaviour outside of the stall

4.3.2.1 Time spent in different behaviours

There was a significant difference between the proportions of time spent by sows from all treatments in different behaviours ($F_{3,156} = 74.30$; $P < 0.001$). When out of the stall, sows from all treatments spent the greatest proportion of time in exploratory behaviour. The proportion of time spent in snout to snout contact was significantly lower than the amount of time spent in other behaviours, with the proportion of time spent in locomotion being equal to the amount of time spent in other behaviours and in snout to snout contact (Fig. 4.2).

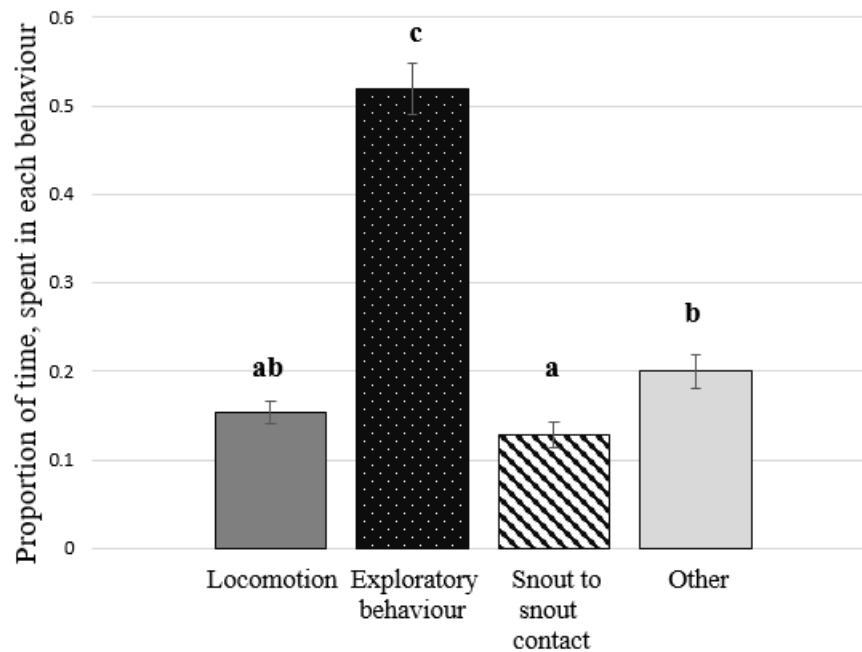


Fig. 4.2. Proportion of time (mean \pm SEM), spent by sows in locomotion, exploratory behaviour, snout to snout contact and in performing other behaviours when outside of the stall. The non-transformed (raw) mean and SEM values are presented. Where superscripts differ, $P < 0.05$.

4.3.2.2 Behaviour when out of the stall in high and low score populations

In the high score population, the percentage of time spent in locomotion was influenced by the opportunity number ($F_{2,39.8} = 12.39$; $P < 0.001$). Sows spent a greater proportion of time in

locomotion during their first opportunity to receive the reward of time out of the stall than in their second ($P = 0.016$) and third opportunities ($P < 0.001$), and the proportions of time spent in locomotion significantly differed ($P = 0.007$) between the second and third opportunities as well (first opportunity: 15.83 ± 0.21 , second opportunity: 12.58 ± 0.23 , third opportunity: 9.24 ± 0.24). Treatment, parity and BCS (Table B.1), as well as FR (Table 4.2), did not affect the percentage of time spent in locomotion by the high score population.

Sows from the high score population spent more time in exploratory behaviour over each FR stage from 21 to 108, in comparison to the FR 9, with proportions of time spent in exploratory behaviour at FR 14 and 162 being intermediate. The proportion of time spent in exploratory behaviour at FR 243 was higher than at all lower FR (Table 4.2). The percentage of time spent in exploratory behaviour at FR 365 was not different from the other FR levels, which is likely due to error as the number of sows that remained on trial at FR 365 was reduced to one sow and hence this data is not presented. Sows from the high score population from 0.5 HF treatment tended ($F_{2,42.6} = 3.18$; $P = 0.052$) to spend more time in exploratory behaviour than control sows, with ad-lib HF sows being intermediate (C: 55.27 ± 8.48 , 0.5 HF: 71.19 ± 9.41 , ad-lib HF: 68.08 ± 9.72). There was no influence of parity, BCS and opportunity number on the percentage of time spent in exploratory behaviour (Table B.1).

Within the high score population, the percentage of time spent in snout to snout contact tended ($F_{2,58.4} = 2.44$; $P = 0.096$) to be influenced by BCS. Sows with BCS 3 tended to spend more time in snout to snout contact than sows with BCS 2, with sows with BCS 4 being intermediate (BCS 2: 6.17 ± 1.27 , BCS 3: 11.49 ± 0.87 , BCS 4: 6.89 ± 1.97). There was no influence of treatment, parity and opportunity number on the percentage of time spent in snout to snout contact in the high score population (Table B.1). FR did not impact the percentage of time, spent in snout to snout contact as well (Table 4.2).

The percentage of time assigned to the category “Other” (including the percentage of time spent performing licking bars, defecating, urinating and being out of sight) in the high score population was influenced by treatment ($F_{2,44.6} = 3.59$; $P = 0.036$) and FR ($F_{9,80.9} = 2.59$; $P = 0.011$). Control sows spent more time in other behaviours than 0.5 HF sows ($P = 0.010$), with ad-lib HF sows being intermediate (C vs ad-lib HF: $P = 0.266$, 0.5 HF vs ad-lib HF: $P = 0.419$; C: 18.02 ± 6.20 , 0.5 HF: 6.84 ± 6.98 , ad-lib HF: 13.21 ± 7.11 , mean percentage \pm SEM). The percentage of time spent in other behaviours by sows from the high score population varied

largely depending on the FR: it was the highest at FR 9, and the lowest at FR 243, with the percentage of time spent in other behaviours at other FR values being intermediate (Table 4.2). However, the FR results should be interpreted with caution due to the decreasing number of sows within each FR level (only two sows represented within the FR 243 and only one sow within the FR 365). Opportunity number tended ($F_{2,37.6} = 3.11$; $P = 0.056$) to influence the percentage of time spent in other behaviours by sows from the high score population. Sows tended to spend more time in other behaviours for their first opportunity to receive the reward of time out of the stall than for their second and third opportunities, which did not differ (first opportunity: 15.61 ± 5.74 , second opportunity: 10.62 ± 5.98 , third opportunity: 11.83 ± 6.34). Parity and BCS did not influence the percentage of time spent in performing other behaviours (Table B.1).

Within the low score population, the percentage of time spent in locomotion was influenced by parity and opportunity number (Table 4.3). Parity 5 sows spent significantly more time in locomotion than parity 4 sows, and parity 2 sows spent significantly less time in locomotion than parity 4 and parity 5 sows, with parity 3 sows being not different from parity 2 and parity 4 sows. For the opportunity number, pigs spent significantly more time in locomotion during their first opportunity to access time out of their stall, than during the second opportunity, and less time during the third opportunity than during both first and second opportunities. Control sows tended to spend less time in locomotion than 0.5 HF sows, with ad-lib HF sows being intermediate (Table 4.3). BCS and FR (Table B.2) did not influence the percentage of time spent in locomotion by the low score population.

Similar to locomotion, the percentage of time spent in exploratory behaviour by the low score population was influenced by parity and opportunity number (Table 4.3). Parity 3 sows spent significantly more time in exploratory behaviour than parity 2, parity 4 and parity 5 sows, which did not differ. For the opportunity number, sows spent significantly more time in exploratory behaviour during their first opportunity, than during the second and third opportunities, but the percentage of time spent in exploratory behaviour did not differ between the second and third opportunities. Treatment (Table 4.3), as well as BCS and FR (Table B.2), did not impact the percentage of time spent in exploratory behaviour.

The percentage of time spent in snout to snout contact in the low score population was significantly influenced by sow parity (Table 4.3) and BCS ($F_{2,55.1} = 7.69$; $P = 0.001$). In contrast to exploratory behaviour, parity 3 sows spent less time in snout to snout contact, than parity 2 (P

= 0.020), parity 4 ($P = 0.001$) and parity 5 sows ($P = 0.041$), which did not differ (parity 2 vs parity 4: $P = 0.101$, parity 2 vs parity 5: $P = 0.519$; parity 4 vs parity 5: $P = 0.745$). Sows with BCS 3 spent more time in snout to snout contact than sows with BCS 2 ($P = 0.003$) and BCS 4 ($P = 0.004$), which did not differ ($P = 0.299$; BCS 2: 7.90 ± 6.14 , BCS 3: 22.20 ± 3.40 , BCS 4: 10.56 ± 4.61 , mean percentage \pm SEM). There was no influence of treatment, opportunity number (Table 4.3) and FR (Table B.2) on the percentage of time, allotted to snout to snout contact.

The percentage of time spent in other behaviours in the low score population was affected by sow treatment and opportunity number (Table 4.3). Control sows spent more time performing other behaviours than 0.5 HF sows, with ad-lib HF sows being intermediate. Sows spent more time in other behaviours when outside of the stall in their first opportunity than in their second and third opportunities, which did not differ. Parity (Table 4.3), BCS and FR (Table B.2) did not influence the percentage of time, spent in other behaviours.

Table 4.2. Percentage of time (mean \pm SEM) spent in locomotion, exploratory behaviour, snout to snout contact and in other behaviours at different stages of testing by sows from the high score population (sows that reached a minimum FR of 72; n = 15). The results for FR 365 were omitted as this FR was represented by only one sow. The non-transformed (raw) mean and SEM values are presented. Where superscripts differ, $P < 0.05$.

Beha- viour	FR									F-value	P-value
	9	14	21	32	48	72	108	162	243		
	N										
	15	15	15	15	15	15	8	4	2		
Loco- motion	15.95 \pm 1.88	14.55 \pm 1.90	15.20 \pm 1.88	14.67 \pm 1.95	12.60 \pm 1.99	13.42 \pm 2.16	11.68 \pm 2.87	14.95 \pm 3.72	8.30 \pm 5.77	0.58	0.812
Explo- ratory behaviour	49.14 \pm 8.16 ^a	56.09 \pm 8.18 ^{ab}	64.66 \pm 8.16 ^b	64.60 \pm 8.24 ^b	64.49 \pm 8.33 ^b	58.26 \pm 8.55 ^b	64.07 \pm 9.67 ^b	63.63 \pm 11.19 ^{ab}	93.20 \pm 15.36 ^c	2.02	0.048
Snout to snout contact	5.06 \pm 3.50	8.26 \pm 3.52	9.27 \pm 3.50	7.99 \pm 3.56	6.10 \pm 3.64	9.68 \pm 3.94	8.44 \pm 4.62	7.44 \pm 5.36	13.91 \pm 11.53	0.96	0.476
Other	29.34 \pm 5.90 ^a	21.24 \pm 5.92 ^{ab}	12.59 \pm 5.90 ^c	13.93 \pm 6.00 ^{bc}	18.77 \pm 6.08 ^{bc}	19.84 \pm 6.32 ^{ac}	16.46 \pm 7.52 ^{bc}	14.34 \pm 9.04 ^{bcd}	4.63 \pm 2.48 ^d	2.59	0.011

Abbreviations: FR, fixed ratio.

Table 4.3. Percentage of time (mean \pm SEM) spent in locomotion, exploratory behaviour, snout to snout contact and in other behaviours by sows from the low score population (sows that reached the maximum FR of 48; n = 27). The non-transformed (raw) mean and SEM values are presented. Where superscripts differ, $P < 0.05$. * Tendency: $P < 0.10$.

Beha- viour type	Treatment			F- value	P- value	Parity				F- value	P- value	Opportunity number			F- value	P- value
	C	0.5 HF	ad-lib HF			2	3	4	5			1	2	3		
	N															
	7	9	11			11	7	7	2			27	24	22		
Loco- motion	15.22 \pm 2.42 ^{a*}	18.02 \pm 2.46 ^{b*}	15.47 \pm 2.88 ^{ab*}	2.46	0.098	10.84 \pm 2.24 ^a	9.54 \pm 2.92 ^{ab}	15.44 \pm 3.34 ^b	29.14 \pm 3.93 ^c	10.01	< 0.001	20.40 \pm 2.31 ^a	16.20 \pm 2.36 ^b	12.11 \pm 2.35 ^c	12.58	< 0.001
Explo- ratory behaviour	41.04 \pm 6.78	53.88 \pm 6.89	49.18 \pm 8.08	1.56	0.219	50.01 \pm 6.19 ^a	68.36 \pm 8.35 ^b	40.91 \pm 9.59 ^a	32.86 \pm 11.49 ^a	3.82	0.014	41.91 \pm 5.95 ^a	48.64 \pm 6.16 ^b	53.56 \pm 6.65 ^b	3.37	0.044
Snout to snout contact	14.46 \pm 3.87	16.41 \pm 3.90	9.78 \pm 4.43	2.30	0.110	12.24 \pm 3.59 ^a	5.12 \pm 4.58 ^b	20.07 \pm 5.12 ^a	16.78 \pm 6.11 ^a	4.62	0.006	10.69 \pm 43.40	14.47 \pm 3.72	15.50 \pm 3.92	1.34	0.273
Other	28.44 \pm 4.46 ^a	12.69 \pm 4.70 ^b	23.87 \pm 5.66 ^{ab}	4.09	0.022	27.11 \pm 3.82	17.91 \pm 5.68	20.44 \pm 6.95	21.21 \pm 8.80	1.13	0.342	26.47 \pm 3.75 ^a	20.59 \pm 4.19 ^b	17.94 \pm 4.63 ^b	4.25	0.021

Abbreviations: C, control; HF, high fibre.

4.4 Discussion

The present study evaluated how a dietary treatment designed to influence sow satiety affected the motivation of stall-housed gestating sows to exit their stall for a reward of time loose in the alleyway between stalls. The results indicate that the motivation of sows to leave their stall decreased as sow satiety increased. The motivation of sows to receive additional food is influenced by the level of satiation (Souza da Silva et al., 2013). This suggests that sows associated the opportunity to leave their stall not only with the opportunity to exercise but with the opportunity to perform exploration as well. This is further indicated by the fact that sows spent the greatest proportion of time in exploratory behaviour, which included feed seeking and exploring the environment, when out of the stall, compared to other behaviours. Performing a certain amount of feed searching was an expected outcome for 0.5 HF and control sows, considering that food is a resource of a known high value (Patterson-Kane et al., 2011). Sows are particularly motivated to forage as in commercial conditions they are feed-restricted (D'Eath et al., 2018) to as low as 50% of their ad-lib intake (Whittemore et al., 1977). Moreover, because food is essential for survival, a strong innate behavioural drive to forage exists. This drive results in the presence of feed searching motivation even when food is freely available elsewhere (Dawkins, 1990).

Another aspect which needs to be considered when assessing the feeding motivation in sows receiving high fibre, is the timing of measuring motivation and/or behaviour observations in relation to the feeding schedule. In the current study measuring motivation to leave the stall and additional behaviour observations when out of the stall were performed right after sows finished their high fibre meal (for ad-lib HF group), or the waiting time for the operant testing after finishing a meal was carefully calculated (for 0.5 HF sows), so the conclusions about sow motivation to leave the stall and to forage can be made only for the short period after the meal. Ramonet et al. (2000) found that sows receiving high- and low-fibre diets did not differ in their feeding motivation measured over a medium (4.5 h) and long-term (23 h) period after a meal. These results suggest that supplementation of the sows' diet with high fibre can decrease the feeding motivation only temporarily.

Sows from all three dietary treatments interacted with the panel and reached the required FR up to a certain point, indicating that all of them were not only capable of learning the task but also had a certain level of motivation to leave their stall, which is in agreement with the findings

of our study described in Chapter 3. This indicates that even though diet influences the level of motivation to exit the stall, there remains a certain level of motivation in sows at all satiety levels that could represent the need for a greater freedom of movement.

The latency to make the first AB push was not affected by the level of satiety or BCS. This is in agreement with the results of the previous study assessing sow motivation described in Chapter 3, in which we found that the latency to make the first AB push was not influenced by the reward type, prior stall experience of the animal (gilt or sow) or BCS. Elmore et al. (2012) found that the HPP was significantly higher for food than for other resources (compost and straw), but the latency to press the operant panel for all three resources did not differ. All this evidence brings into question the sensitivity of the latency to interact with the operant panel as a measure of motivation.

Sows from all treatments maintained a good level of precision pressing the AB, which was comparable to the previous work described in Chapter 3, which examined sows' motivation to exit the stall. This confirms that the sows were effectively trained and understood that pressing the AB resulted in a reward.

The results on how sows behaved when out of the stall are in agreement with the previous work on sow motivation for a greater freedom of movement (Chapter 3), with sows from all treatments spending the greatest proportion of time outside of the stall in exploratory behaviour and lower proportions of time in locomotion and snout to snout contact. Of particular interest in the current study, fully satiated sows from the ad-lib HF treatment still allotted the highest proportion of their time when out of the stall to exploratory behaviour. This leads to the conclusion that exploratory behaviour is more related to the intrinsic need for exploration in general, which is known to be particularly strong in feed-restricted pigs housed in barren environments (Tuytens, 2005), than to the basic desire to obtain food. This idea can be supported by the study of Jensen et al. (2012), who found that gestating sows receiving semi ad-lib amount of high-fibre diet (ad-lib access to feed during six one-hour periods throughout the day) had a decreased motivation to obtain a feed reward in the operant conditioning test in comparison to pregnant sows fed a restricted diet with or without the addition of high fibre once daily. Similarly, Robert et al. (1997) reported that gilts receiving energy-balanced and low energy high-fibre diets had reduced operant performance when assessing their feeding motivation, in comparison to gilts fed a concentrate diet. Based on this information, it could be

assumed that if feeding motivation was the primary reason of performing exploratory behaviour in the current study, a decrease in performing this behaviour when out of the stall in sows receiving high fibre additional to the standard ration would be observed. However, the results of the current study did not show such a decrease, which further supports the idea of the presence of strong motivation to explore in sows at all satiety levels. Equal proportions of time spent in locomotion and snout to snout contact in all treatments suggest that sows have basic needs for exercise and for social interaction, which are not dependent on their satiety level. These findings are supported by previous research on sow motivation to exit the stall, which revealed that bred female pigs spent considerable proportions of time out of their stall in locomotion and snout to snout contact, with equal proportions of time spent in each of these behaviours within both gilts and sows (Chapter 3).

The results of the separate analysis of behaviours for high score and low score populations of sows show that in sows from both of these populations the proportion of time spent in locomotion, per testing session, was greatest upon the first release from the stall, and decreased thereafter. These findings are in agreement with the result of the previous study on sow motivation for a greater freedom of movement (Chapter 3), and suggest the presence of a rebound effect, as sows showed a strong initial response which could indicate a rebound response to prolonged confinement (Dawkins, 1988). Similar to our study described in Chapter 3, sows expressed the desire to leave the stall every day when given an opportunity. It supports the idea of an intrinsic need for a greater freedom of movement in sows, with such factor as an exploratory drive contributing to the motivation to leave the stall. The presence of these needs suggests that a more complex solution, rather than just providing an opportunity for movement, is necessary in order to improve the welfare of gestating sows. For example, such factors as appropriate housing space design, providing opportunities to interact with conspecifics and to perform natural behaviours, as well as provision of environmental enrichment need to be considered (Bench et al., 2013). In the low score population, the percentage of time spent in locomotion increased with sow parity, which might be due to an increased need for movement in ageing animals, or it can be because older and hence larger sows experience lower levels of comfort in conventional gestation stalls. The latter explanation is in agreement with the findings of Rioja-Lang et al. (2013), who discovered that if having a choice between stalls and free space area in a free access stall housing system, mid parity sows spend more time in the free space area

than young sows. That control sows from the low score population had a tendency to spend less time in locomotion in comparison to sows receiving high fibre feed may be due to prioritizing feed searching by feed-restricted sows. This finding further suggests that providing high fibre feed to gestating sows can decrease their activity level, and is in agreement with the study of Ramonet et al. (1999), which found that pregnant sows fed a high-fibre diet (18.1% crude fibre) spent less time standing in comparison with sows fed a conventional diet, which was low in crude fibre (3.3%). Similarly, Bergeron et al. (2000) demonstrated that sows fed very high-fibre (23.0% crude fibre) and high-fibre diet (18.2% crude fibre) spent more time lying and less time standing during a 12 h observation which included both morning (60% of the daily ration) and afternoon (40% of the daily ration) feedings, than control sows receiving ration containing 5.3% of crude fibre. Sows fed very high-fibre ration were also found to lay more than control sows during the 2 h period post feeding in the afternoon. Furthermore, the lower activity level in sows from very high-fibre treatment in the study of Bergeron et al. (2000) was confirmed by performing fewer stereotypies in comparison to control sows, with sows receiving the intermediate amount of high fibre being no different from two other treatments. Similarly, Zonderland et al. (2004) showed that sows fed a restricted amount of low-fibre diet (5.9% crude fibre) were less inactive and lay ventrally less, but also performed more self- and substrate-directed behaviours, as well as stood and moved more than sows receiving high-fibre diet (13.2% crude fibre) ad-libitum. Terlouw et al. (1991) reported similar results, including the higher total level of activity and higher performance of chain-related and bar-oriented activities in feed restricted (2.2 kg of feed/day) pregnant gilts in comparison to gilts fed at a high level (4.0 kg of feed/day). Interestingly, high-fed gilts from the study of Terlouw et al. (1991) did not receive high-fibre feed, but their activity levels were decreased, similarly to the current study and to the study of Bergeron et al. (2000), which provides further evidence on the presence of a link between feeding high-fibre feed and satiety. However, the limitation of the current study is that sow postures and levels of stereotypies were not recorded in stalls and stereotypies were not recorded when out of the stall. Hence, only levels of general activity measured out of the stall in the current study could be compared to previous literature.

The percentage of time spent in exploratory behaviour by sows from the high score population increased as the FR increased, and is in agreement with our previous findings, described in Chapter 3. The increase in exploratory behaviour can be explained by the presence

of an initial period of habituation to the testing routine (low % time spent in exploration at FR 9), and then by maintaining high levels of exploration at higher levels of FR, which included feed searching as a predominant behaviour in the behavioural repertoire of swine (Stolba and Wood-Gush, 1989). However, the effects of FR on sow behaviour in both high and low score populations may be less reliable and should be interpreted with caution, as the change in behaviours over the increasing FR schedule may be due to a decreasing number of sows left on trial as the FR increased. The percentage of time spent in exploratory behaviour by the low score population in this study increased over the course of the three opportunities for time out of the stall within one testing session, which is in agreement with the previous findings described in Chapter 3. This finding is unlikely related to an increase in levels of hunger over the course of the testing session, as sows from 0.5 HF and ad-lib HF treatments consumed their high fibre rations shortly before the session, hence it can be assumed that their levels of satiety remained unchanged during the testing. The fact that sows in their third parity spent more time in exploratory behaviour than younger and older sows suggests that sows of this age group need opportunities for exploration and seeking additional food more than others, but the reasons of this age-specific motivation remain unclear. Furthermore, third parity sows spent the lowest proportion of time in snout to snout contact in comparison to other age groups, which suggests that these sows are having a higher income elasticity of demand for seeking social contact in comparison to lower income elasticity of demand for exploratory behaviour (Dawkins, 1990), which further highlights the dominance of exploratory and feeding motivation in sows from this group.

The results for snout to snout contact in the low score population also showed that sows with ideal body condition score were more social than thin and over-conditioned sows. These findings, which are in agreement with our previous study discussed in Chapter 3, support the idea that feeding motivation is dominant in thin sows, and that these sows are willing to satisfy this primary need at cost of secondary needs, such as a need for social contact. Low levels of snout to snout contact observed in over-conditioned sows may be a result of reduced musculo-skeletal fitness due to excessive body weight, or they may be due to lower income elasticity of demand for feed searching behaviour in these sows: over-conditioned sows may have a stronger motivation for feed-searching than thinner sows, hence they allot more time to feed searching at the cost of social interaction. The tendency for fully satiated sows to be less social in comparison

to less satiated sows may be due to the general lower desire to move when digesting high fibre feed in large quantities, which may be caused by an increase in weight of gastrointestinal tract (Kass et al., 1980). However, an emotive component, such as a feeling of calm and wellness when fully satiated, could also be possible, and it needs to be further explored. However, the effects of BCS need to be interpreted with caution, as the groups of sows with BCS 2 and BCS 4 were represented by the low numbers of animals (BCS 2: n = 4; BCS 4: n = 7).

4.5 Conclusions

Stall-housed gestating sows experiencing different levels of satiety were motivated to exit their stall, as determined by the HPP. The strength of motivation to leave the stall was influenced by sow satiety level and this motivation decreased as sow hunger decreased. However, regardless of dietary treatment, all sows worked to achieve time out of the stall, and when out of the stall they spent a certain amount of time in locomotion. The presence of a possible rebound effect in performing locomotor behaviour within the testing session in sows from both high and low score populations suggests that sows have an intrinsic need for exercise. The behaviour of sows when out of the stall provides evidence for the presence of strong motivation for exploration regardless of satiation, indicating a strong innate exploratory drive. The evidence collected in this study suggests that the provision of high fibre feed in addition to the standard gestation ration can decrease sows' motivation to leave the stall. This effect of high fibre feed provision could contribute to increasing stall-housed sow welfare if providing access to time out of the stall is not viable, or it could decrease the amount of time out of the stall that is needed. However, in order to achieve optimal levels of welfare, sows require access to enrichment and opportunities for exploration in addition to addressing hunger. Giving sows opportunities for exercise and social interaction should also be considered.

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5. THE EFFECT OF PROVIDING A GREATER FREEDOM OF MOVEMENT THROUGH PERIODIC EXERCISE ON THE WELFARE AND STRESS PHYSIOLOGY OF STALL-HOUSED GESTATING SOWS AND PIGLET BEHAVIOUR

The findings presented in Chapters 3 and 4 indicated the presence of a motivation to leave the stall in gestating female pigs, the strength of which depends on sow satiety level. These results suggest that sows have an intrinsic behavioural need for movement. However, whether satisfying this need through providing periodic exercise can improve sow welfare needs to be explored. In Chapter 5, the effects of providing periodic exercise on the welfare and stress physiology of stall-housed gestating sows and piglet behaviour were explored and compared to the measures obtained from stall-housed sows receiving no exercise and group-housed sows. The results show that group housing, but not periodic exercise improved sow comfort and reduced stress, as indicated by sow postures and stereotypy levels. A more proactive piglet behavioural response observed in sows without access to a greater freedom of movement indicates that gestation housing can influence the behaviour of offspring.

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Abstract

In Canada, the 2014 Code of Practice for the Care and Handling of Pigs proposed to continue the operation of existing stall barns after 2024 if bred sows housed in these barns have access to a greater freedom of movement, for example through being periodically exercised. Therefore, this study evaluated the effects of periodic exercise on sow welfare. Sows ($n = 180$) were assigned to one of three treatments: stall-housed (Control: C), stall-housed and weekly exercised (Exercise: E; 160 m/session), group-housed (Group: G). Sow postures and stereotypies were recorded once/week in early, mid and late gestation (weeks 2, 10, 15) before (AM) and after (PM) exercise. Female piglets ($n = 168$ from 17 C, 20 E and 20 G sows) underwent behavioural tests on 19-22 day of age. Postures differed by treatment with G sows lying more and sitting less than C and E sows in AM, which did not differ. In PM, E sows sat more than G sows, with C sows being intermediate. Stereotypies: in early gestation, G sows performed fewer stereotypies than E sows, with C sows being intermediate. In mid gestation, G sows performed fewer stereotypies than C and E sows, which did not differ. Piglets from C sows were more active than E and G piglets, which did not differ. Group housing improved sow comfort (indicated by postures) and reduced sow stress (indicated by stereotypies), but periodic exercise did not. A more proactive piglet behavioural response in sows without access to greater freedom of movement was observed indicates implications for gestation housing to influence the behaviour of offspring.

Keywords: animal welfare, gestation stall, hair cortisol, periodic exercise, pig, prenatal stress.

5.1 Introduction

Confinement of sows in gestation stalls remains one of the major welfare concerns in the pork industry (Kim et al., 2016). Gestation stalls are negatively perceived by society due to the restriction of sow movement, as well as foraging and social behaviour for prolonged periods of time (Tonsor et al., 2009). Due to these circumstances, gestation stalls are being actively phased out around the world, and changes towards sow group housing are set in motion. Previous studies suggest that stall-housed sows are motivated to leave the stall, and when out of the stall, they show a rebound response to prolonged confinement demonstrated by spending the greatest proportion of time in locomotion during the first opportunity to leave the stall in comparison to two subsequent consecutive opportunities within the same testing session, as described in Chapters 3 and 4. These findings indicate the presence of an intrinsic behavioural need for

movement, and it is considered that accommodating this behavioural need would lead to an improvement of sow welfare (Stolba and Wood-Gush, 1984).

In Canada, the Code of Practice for the Care and Handling of Pigs (NFACC, 2014) proposes a grandfather clause that existing stall barns in good working order, constructed before 2014 may continue to house gestating female pigs in gestation stalls, if these animals are provided with opportunities for a greater freedom of movement, such as periodic exercise. Previous research indicated that providing intensive periodic exercise to stall-housed gestating sows can bring physiological benefits (Schenck et al., 2008; Harris et al., 2013), in comparison to housing in stalls without access to exercise. However, whether periodic exercise can improve sow welfare by reducing the stress of animal confinement and how beneficial is providing exercise at low levels which is more realistic in commercial conditions, is unknown. Previous studies have shown that group-housed sows have lower levels of stereotypies, reduced restlessness and lower lameness scores than stall-housed sows (McGlone, 2013). To understand how periodic exercise compares to other methods of managing gestating sows, a comparison of welfare measures of stall-housed sows receiving periodic exercise to those of stall-housed sows and those group-housed is needed.

When comparing housing systems that provide different levels of freedom of movement (stall-housing and group-housing with different space allowances), previous research found differences in sow behaviour that suggests welfare changes (Weng et al., 2009; Chapinal et al., 2010). In particular, that sows housed in stalls had a higher frequency of sitting in comparison to sows in groups, suggesting reduced comfort levels (Weng et al., 2009), and that restrict fed sows performed a greater amount of stereotypies (sham chewing and oronasofacial behaviours) when housed in stalls, than groups (Chapinal et al., 2010), providing evidence for the role the environmental restriction plays in contributing to stereotypy development. This evidence suggests that sow behaviour can be used as an indicator of sow welfare across different housing systems.

If stall-housed pregnant sows are experiencing gestational stress, it is most likely to be chronic. Yet previous studies have focused on assessing acute stress responses, such as measuring levels of circulating cortisol (McGlone, 2013). This has made evaluation of sow welfare in different housing systems quite challenging; when acute measures have been measured, it has commonly been found that there is no difference (Karlen et al., 2007), but this

may be because the type of stress experienced by gestating sows is different in group and stall systems. Evaluating for the effects of chronic prenatal stress, which affects both pregnant dams and their offspring, could be an alternative and sensitive measure to evaluate how a gestation system effects sow welfare, for stressors experienced by the sow during gestation alter the behavioural responses of piglets to stressors (Kranendonk et al., 2007; Brajon et al., 2017).

The objectives of this study were to determine the effects of providing periodic exercise to stall-housed sows throughout gestation on sow welfare, as evaluated through the measurement of sow behaviour, stress physiology and measures of prenatal stress, as measured in the offspring behaviour. Additionally, these measures were compared to those obtained from stall-housed sows receiving no exercise and group-housed sows.

5.2 Materials and methods

All experimental procedures were approved by the University of Saskatchewan Animal Care Committee (#20170057), which is regulated by the Canadian Council of Animal Care (2009). This experiment was conducted between February and November of 2019 at the Prairie Swine Centre, Saskatoon, Canada.

5.2.1 Animals and husbandry

A total of 180 Camborough 42 sows (parities 0-7, 2.42 ± 1.76 , mean \pm standard deviation [SD]) were studied. Animals were housed in free-access stall gestation pens (Egebjerg INN-O-STALL® free access stalls, Egebjerg International A/S, Nykøbing Sjælland, Denmark). Each free-access stall pen contained 32 free access stalls, each 0.65 m by 2.1 m in size, 16 stalls on adjacent sides of the pen, with a 3.0m wide fully slatted loafing alleyway in between. The design of the free-access stall pens is described in more detail in Rioja-Lang et al. (2013). For experimental purposes, each gestation pen was divided into two halves with a central divider, so there were eight stalls on adjacent sides of each half of the pen. Sows were moved to gestation pens on day 7-10 post breeding and remained in the gestation room until day 107-110 of gestation. A total of 12 experimental animals were selected within one breeding week, forming one replicate block, with a total of 15 replicate blocks. Body condition score (BCS) was determined and recorded for each experimental animal. Sows were fed approximately 2.2 kg of a

standard sow gestation diet once per day at 0700 h, and each individual stall and group loafing area were equipped with nipple drinkers.

On day 107-110 of gestation, sows were moved to standard farrowing crates equipped with electronic sow feeders and nipple drinkers. Farrowing was allowed to occur naturally, with limited intervention by trained personnel if a piglet birth interval was longer than 3 h. The piglets had access to a lit and heated location at the front of the farrowing crate, which was inaccessible to the sow. Cross-fostering occurred within two days of age and was performed in accordance with the barn practices to maintain a litter size of 14 piglets per sow. Fostered piglets were not used for behavioural testing in the current study. Commercial husbandry procedures performed by the barn staff on the piglets included teeth clipping (at one day of age), as well as ear notching, tail docking, iron injections and castrations with an analgesic of injectable meloxicam (at three days of age). Additionally, ear tagging was performed in those piglets that were used for behavioural testing.

On day 1 after birth, three female piglets per sow from 17 control sows (distribution by parity group: young: n = 5; mid: n = 8; old: n = 4), 20 exercise sows (young: n = 2; mid: n = 14; old: n = 4) and 20 group sows (young: n = 7; mid: n = 12; old: n = 1) were selected for behavioural testing. The original aim was to test piglets from 20 sows per treatment, but three control sows had to be removed from trial due to illness or not being pregnant. Out of 57 selected sows, three sows had only two female piglets, hence for these animals, two piglets were used for behavioural testing. Behavioural testing was performed on day 19-22 after birth, and a total of 168 piglets were tested.

5.2.2 Treatments

Upon moving to gestation pens, sows were assigned to one of three treatments (four sows per treatment per replicate, n = 180 sows, 60 per treatment): sows housed in stalls throughout gestation (control: C); stall-housed sows given weekly exercise throughout gestation (exercise: E); sows housed in static groups after breeding (group: G). All treatments were balanced by parity and represented within the same gestation pen, with individual sow as the experimental unit. Two replicates were represented within each pen, as the central divider prevented two replicate groups from mixing.

Sows from C treatment stayed locked in the free-access stalls throughout gestation. Sows from E treatment were also locked in stalls throughout gestation, except when removed for exercise. To provide exercise, E sows were backed out of their stalls once a week, walked out of the gestation pen and walked in a loop twice around the alleyways surrounding half of the gestation room (Fig. 5.1). Exercise was performed between 1100 h and 1300 h on the same day each week. The distance travelled by each sow during one exercise session was approximately 160 m, and the duration of one exercise session was approximately 10 mins. Sows were encouraged to keep moving by the handler through vocal cues, and, if needed, taps from the hand and use of a pig board. Sows were exercised one at a time before being returned to their stall. Sows from G treatment were locked out of the free access stalls for 6-7 hours a day, remaining in the group loafing area (3.0 m × 5.35 m; 4.01 m² per sow) with concrete slatted floor, and having free access to the stalls and the loafing area during the rest of time. G sows were locked in the stalls once a week whilst E sows were being exercised.



Fig. 5.1. Sow exercising in the gestation room alleyway.

5.2.3 Sow behavioural observations

A camera (Pentax Optio W90 12.1, Denver, CO, USA), was mounted on the ceiling in the alleyway near each experimental pen to record the stalls containing C and E sows, and the loafing area, containing G sows, was programmed to take photos at 10-minute intervals. The pictures were collected over two intervals, on the same day that exercise provision occurred for E sows: AM data collection; 2 hrs in the morning before exercise from 0900 h to 1100 h, and PM data collection; 1.5 hrs in the afternoon after exercise from 1300 h to 1430 h. Pictures were collected at three stages of gestation: early (week 2 post breeding), mid (week 10 post breeding) and late gestation (week 15 post breeding). Prior to the start of recording, numbers were sprayed on the back of each experimental sow for individual identification. The pictures were viewed by scan sample with individual sow postures recorded (Table 5.1).

Sows were live-scored for stereotypic behaviours at three stages of gestation on the same days when the recordings of sow postures took place. During the data collection, the observer was sitting quietly on a ladder above the level of sow stalls at the end of the aisle between pens, so all the observed animals were visible. Similarly to the posture data collection, sows were observed during two periods each day: a 1 h period in the morning before exercise and after feeding (0900 h to 1000 h, AM data collection), and a 1 h period in the afternoon after exercise (1330 h to 1430 h, PM data collection). A 2-minute interval scan-sampling technique (Martin and Bateson, 1993) was used to record the presence of stereotypic behaviours (Table 5.1).

Table 5.1. Sow postures and stereotypic behaviour recorded in early (week 2 post breeding), mid (week 10 post breeding) and late gestation (week 15 post breeding) in each of three treatments: control sows housed in individual stalls throughout gestation (n = 53), stall-housed sows given exercise (160 m per week) during gestation (exercise; n = 58), and sows housed in groups throughout gestation (group; n = 58). Adapted from Chapinal et al. (2010) and Zhang et al. (2017).

Category of behaviour	Description
Posture	
Lying	The animal is lying down with or without a head in contact with the floor and non-weight bearing on its limbs. Both lateral (lying on the side) and sternal (lying on the abdomen) lying were included.
Standing	The animal is standing up with all four claws in contact with the floor/other objects and weight bearing on all four limbs.
Sitting	The animal is sitting up with front legs extended and weight on the rump.
Stereotypic behaviour	
Sham chewing	Continuous chewing with no substrate present in the mouth.
Bar-biting	Nosing, rubbing, licking or biting any metal component of the stall other than the trough.
Tongue-rolling	Extending the tongue out of the mouth and curling it to the side, without the tongue contacting any object.
Trough manipulation	Nosing, rubbing, licking or biting the trough.

5.2.4 Chronic stress: hair cortisol analysis

To investigate the value of hair cortisol as a non-invasive longer-term marker of HPA axis activity, hair samples from sows in each treatment (C: n = 17; E: n = 20; G: n = 20), were collected and analysed. The original aim was to collect hair samples from 20 sows per treatment, but three control sows had to be removed from trial due to illness or not being pregnant. Hair was shaved at weaning from the loin part of the dorsolumbar region from a maximum area of

100 cm² and then reshaved before sows entered the trial to achieve the maximal removal of hair growth from the previous lactation. At day 107-110 of gestation upon moving to the farrowing crate, the hair regrowth from the preshaved area was collected and processed for cortisol analysis. Hair was collected by shaving close to the skin with electric clippers, which were cleaned with a brush between sows. Once sampled, hair was stored at room temperature inside paper envelopes until it was analysed.

For hair sample preparation and cortisol extraction, the protocol developed by Macbeth et al. (2010) was used. Methanol was used as wash solvent, as determined to be most appropriate for removing external contaminants from swine hair (Pollock et al., unpublished results). First, hair samples were mechanically cleaned with forceps to remove gross contaminants (manure), and 100 mg samples of cleaned hair were weighed out. Eleven samples were lighter than 100 mg, and these samples were also prepared for cortisol extraction as described below, with the volume of methanol added being reduced proportionally. Each sample was washed in 4 ml (for the 100 mg hair samples) of methanol three times. The washing procedure involved rotating the hair samples in the haematology mixer at 12 rpm for 3 mins per wash, and then the samples were allowed to dry in plastic petri dishes at room temperature. After a minimum of 24 hrs drying, samples were ground into a fine powder with a Retsch MM 301 Mixer Mill (Retsch, Inc., Newton, PA, USA) at 30 Hz. For the 100 mg samples, the grinding time was 0.03 mins per mg of hair, and 10 ml stainless steel grinding jars with a 12 mm grinding ball were used; for samples lighter than 100 mg the grinding time was 0.15 mins per mg of hair, and 5 ml stainless steel grinding jars with a 7 mm grinding ball were used. After grinding, 25 mg samples of ground hair were weighed out and transferred to 0.6 ml microtubes and stored at room temperature out of direct sunlight.

For cortisol extraction, 0.5 ml of HPLC grade methanol was added to each sample, which was then vortexed for 10-15 s and placed on an automatic rotator at 18 rotations per minute for 24 hrs. Afterwards, the samples were spun in a centrifuge at 4500 rpm for 15 minutes. The entire supernatant was transferred to the bottom of a glass 12 × 75 mm test tube and dried under a gentle stream of nitrogen gas at 38 °C. The extraction procedure was repeated for three collections in total to ensure that all steroids were recovered. Next, steroids were rinsed to the bottom of the test tubes with three consecutive methanol washes (0.4, 0.2 and 0.15 ml of methanol) and dried under a gentle stream of nitrogen gas at 38 °C after each wash. Concentrated

samples were reconstituted with 0.2 ml of phosphate wash buffer, vortexed on the lowest setting for 10 s, incubated at 4 °C for 12 hours, and repeatedly vortexed for 40 s. Samples were centrifuged for 2 mins at 4000 rpm and 20 °C, transferred to 0.6 ml plastic vials and spun at 4500 rpm for 5 mins. The supernatants were collected and analysed with a commercially available EIA kit (Salimetrics® High Sensitivity Salivary Cortisol Enzyme Immunoassay kit; Salimetrics LLC, State College, PA, USA). The kit has previously been validated for use for the cortisol analysis in swine hair by Casal et al. (2017). Cross-reactivity of the antibody used for the EIA kit according to the manufacturer was: prednisolone (0.57%), cortisone (0.13%), 11-deoxycortisol (0.16%), dexamethasone (19.2%), corticosterone (0.21%), triamcinolone (0.09%). All other intermediates and hormones reported by the manufacturer exhibited cross-reactivity of $\leq 0.04\%$.

5.2.5 Piglet behavioural testing

As an additional measure of maternal stress, prenatal stress effects on the piglet behavioural response to stress were evaluated via isolation and novel object tests performed on a sub-sample of female piglets on days 19-22 after birth. For the testing, three experimental piglets from each sow were placed in a cart and moved from the farrowing room to the isolated waiting room equipped with a heat lamp; this room was adjacent to the test room. Each piglet was individually carried into the isolated test arena from the waiting room one at a time. The arena had solid concrete flooring measuring 2.36 m x 2.95 m, and solid opaque walls, and was divided into 20 equal-sized squares using lines on the floor. Additionally, two circles with a radius of 0.50 m and 1.00 m were drawn in the centre of the arena. The number of squares visited by a piglet, and the number of vocalizations within the 2-minute isolation test were live-recorded by an experienced observer, blind to treatments. A piglet was considered to have visited a square when the two front legs of the piglet were inside the square. Following cessation of the isolation test, there was a 1-minute break when the piglet was left in the arena, following which a novel object (Bite-Rite toy, Ikadan System A/S, Ikast, Denmark) was placed in the centre of the test arena. The frequency of entering 1.00 m and 0.50 m circles of the novel object, the frequency of exiting the 1.00 m circle and remaining in the area bordering the perimeter of the pen, the number of squares visited, and the number of vocalizations for the novel object test were live-recorded by an experienced observer during the 2-minute test. A piglet was considered to have visited a circle if the piglet changed its position from being outside of a certain circle with all four legs to having

its two front legs inside this circle. The latencies to enter the 1.00 m and 0.50 m circles, the latency to touch the novel object and the number of contacts with the novel object were live-scored by another experienced observer during the 2 mins. After this, the test ended and the piglet was returned to the farrowing pen. Additionally, piglet behaviour throughout the tests was video recorded with a camcorder (Canon Vixia HF R800, Canon Canada Inc., Brampton, ON, Canada) so the sessions could be rewatched if needed to verify information.

5.2.6 Statistical analysis

For the statistical analysis, sows were assigned to one of three parity groups: young (parity 0-1), mid (parity 2-4) and old parity sows (parity 5-7). Data were analysed using the statistical package SAS 9.4 (SAS Institute, Cary, NC, USA). The significance level was set at $P \leq 0.05$, and results with $P < 0.10$ were considered as statistical trends. Residuals of all dependent variables were examined for normality and homogeneity of variance, and the data were transformed as necessary. The least-square means (LSMEANS) of fixed effects with Tukey's adjustment were used to account for multiple comparisons. Results are presented in the mean and SEM from the raw (not transformed) data as computed from the final model. For the main effects, P-values and F-values are presented, and adjusted P-values are presented for post hoc comparisons.

5.2.6.1 Sow behaviour data

To compare postures of sows from control, exercise and group treatments, relative frequencies of lying, standing and sitting out of total observations per data collection period (AM or PM) were calculated per sow, and then analysed in separate models for each posture and each data collection period. To calculate the relative frequency of performing a certain behaviour, the number of times spent in this behaviour during one behavioural observation period (AM data collection or PM data collection) was divided by the total number of behavioural events recorded in this observation, resulting in a proportion. To compare the levels of stereotypies performed in sows across different experimental treatments, relative frequencies of the total of recorded stereotypic behaviours (obtained from summing the numbers of events of performing sham chewing, bar-biting, tongue-rolling and trough manipulation) were calculated and analysed in separate models for each data collection period (AM and PM). A mixed model (PROC MIXED procedure in SAS) with repeated measures of the stage of gestation and sow as a subject was

used for analysing postures and stereotypy data, and simple correlation structure was used. The fixed effects of treatment, parity group and stage of gestation, as well as interactive effects of treatment and stage of gestation, and treatment and parity group were tested. The interactive effect of treatment and parity group was not significant in the posture models and hence it was removed from these models but kept in the stereotypy models. The random effect of replicate was added to the models. The AM sow posture data required square root transformation, and the PM sow posture data required arcsine square root transformation. The AM stereotypy data required arcsine square root transformation, and the PM stereotypy data required square root transformation.

5.2.6.2 Hair cortisol data

A mixed model (PROC MIXED in SAS) was used to compare sow treatments for differences in hair cortisol, with treatment, parity group, BCS and interaction of treatment and parity group as main effects, and total litter size as a covariate. The variable hair cortisol (pg/mg) was not normally distributed, and therefore was log transformed. The effects of parity group, BCS and interactive effects of sow treatment and parity group were not significant and removed from the model.

5.2.6.3 Piglet testing data

To evaluate the effects of sow treatment and parity group on the number of squares visited and the number of vocalizations in the isolation test and for the novel object test, the frequency of entering the 1.00 m and 0.50 m circles in the novel object test, the frequency of exiting the 1.00 m circle and remaining in the area bordering the perimeter of the pen, the latency to enter the 1.00 m and 0.50 m circles, the latency to touch the novel object, and the number of contacts with the novel object, a mixed model (PROC MIXED) was used. If a piglet did not enter a certain circle or did not touch the novel object, it was assigned the maximal latency of 120 s for this measure. The mixed model was the model of choice for the piglet data, as using this model resulted in better fit statistics in comparison to PROC GLIMMIX model with Poisson distribution, which was also tested. Piglet nested within sow and replicate were included as random effects. Each of the variables of interest was analysed in a separate model, and all the variables required log transformation. Parity group did not show a significant association in the

isolation test, and it was removed from the final models for this test. The interaction of treatment and parity group did not have a significant effect for both the isolation test and the novel object test, and hence it was removed from all of the models.

5.3 Results

In total, 12 sows were removed from the trial and their data were not included in the final statistical analysis, nine of these sows aborted (C: $n = 5$; E: $n = 3$; G: $n = 1$), and three sows were removed due to illness (C: $n = 2$; G: $n = 1$). Additionally, the postures data were missing for some replicates over some data collection periods due to a secure digital card malfunction. Given these circumstances, the population of sows included in the analysed data was as follows: AM, early gestation: $n = 146$; AM mid gestation: $n = 157$; AM late gestation: $n = 135$; PM early gestation: $n = 146$; PM mid gestation: $n = 156$; PM late gestation: $n = 134$. For the main effects, P-values and F-values are presented, and adjusted P-values are presented for post hoc comparisons.

5.3.1 Sow behaviour

5.3.1.1 Postures

For sow postures in AM, the relative frequency of lying was influenced by sow treatment ($F_{2,411} = 6.55$; $P = 0.002$), parity group ($F_{2,424} = 7.05$; $P = 0.001$) and stage of gestation ($F_{2,422} = 18.42$; $P < 0.001$). Group sows lay more than control and exercise sows, which did not differ (Fig. 5.2). Young sows spent significantly more time lying, than mid ($P = 0.004$) and old parity sows ($P = 0.001$), for which the relative frequency of lying did not differ ($P = 0.112$; Young: 0.59 ± 0.04 , Mid: 0.49 ± 0.03 , Old: 0.45 ± 0.04 , mean relative frequency \pm SEM). Sows in mid gestation spent more time lying, than sows in early gestation ($P = 0.028$), and sows in late gestation lay more than sows in early ($P < 0.001$) and mid ($P < 0.001$) gestation (Early: 0.41 ± 0.03 , Mid: 0.48 ± 0.03 , Late: 0.63 ± 0.04).

The relative frequency of sitting in AM was influenced by sow treatment ($F_{2,413} = 6.64$; $P = 0.001$) and stage of gestation ($F_{2,421} = 7.56$; $P = 0.001$). Group sows sat less than C and E sows, which did not differ (Fig. 5.2). Sows in early gestation spent less time sitting, than sows in mid ($P = 0.003$) and late ($P < 0.001$) gestation, which did not differ ($P = 0.398$; Early: 0.10 ± 0.02 , Mid: 0.15 ± 0.02 , Late: 0.15 ± 0.02 , mean relative frequency \pm SEM). There was no effect of

parity group ($F_{2,406} = 0.29$; $P = 0.746$) on the relative frequency of sitting (Young: 0.12 ± 0.02 , Mid: 0.13 ± 0.01 , Old: 0.14 ± 0.02). There was also no interactive effect of treatment and stage of gestation on the relative frequency of lying and sitting in AM (Table C.1).

For standing in AM, there was an effect of parity ($F_{2,417} = 4.22$; $P = 0.015$) and an interactive effect of treatment and stage of gestation ($F_{4,412} = 2.71$; $P = 0.030$). In early gestation, C sows tended to spend less time standing, than E sows, but did not differ from G sows, and E sows tended to stand more, than G sows. In mid gestation, C sows tended to stand more than E sows, with G sows being intermediate. In late gestation, C sows stood more, than G sows, with E sows being intermediate (Fig. 5.3). Also, C sows spent more time standing in early, than in late gestation ($P = 0.007$). In early gestation, E sows stood more than in mid and late gestation ($P < 0.001$). Exercised sows in mid gestation tended ($P = 0.054$) to stand more, than in late gestation. Group sows in late gestation stood less ($P < 0.001$), than in early and mid gestation.

Young sows spent significantly less time standing in AM than mid ($P = 0.007$) and old sows ($P = 0.027$), for which the proportion of time spent standing did not differ ($P = 0.767$; Young: 0.28 ± 0.03 , Mid: 0.37 ± 0.02 , Old: 0.39 ± 0.04 , mean relative frequency \pm SEM).

Within PM measurements, the relative frequency of lying did not differ by treatment effect (Table C.2), and there was no interaction between treatment and stage of gestation (Table C.1). Parity group tended ($F_{2,424} = 2.49$; $P = 0.084$) to affect the relative frequency of lying, with old sows lying less than young sows, and mid sows being intermediate (Young: 0.72 ± 0.04 , Mid: 0.68 ± 0.03 , Old: 0.63 ± 0.05). The relative frequency of lying in PM was affected by the stage of gestation ($F_{2,423} = 7.40$; $P = 0.001$). Sows in early gestation lay less than in mid ($P = 0.040$) and late gestation ($P < 0.001$), and there was a tendency ($P = 0.053$) for sows in late gestation to lie more than in mid gestation (Early: 0.60 ± 0.04 , Mid: 0.68 ± 0.03 , Late: 0.75 ± 0.04).

There was an effect of treatment on the relative frequency of sitting in PM ($F_{2,424} = 10.93$; $P < 0.001$). E sows sat more than C ($P = 0.025$) and G sows ($P < 0.001$), and C sows sat more, than G sows ($P = 0.021$; C: 0.08 ± 0.01 , E: 0.12 ± 0.01 , G: 0.04 ± 0.01 , mean relative frequency \pm SEM). There was no effect of parity group on the relative frequency of sitting in PM ($F_{2,424} = 1.08$; $P = 0.340$; Young: 0.07 ± 0.01 , Mid: 0.07 ± 0.01 , Old: 0.10 ± 0.02). There was also no effect of the stage of gestation (Table C.2) and no interactive effect of treatment and stage of gestation on the relative frequency of sitting in PM (Table C.1).

There was no effect of treatment on the relative frequency of standing in PM (Table C.2), but it was influenced by sow parity group ($F_{2,424} = 3.98$; $P = 0.019$) and by the stage of gestation ($F_{2,423} = 5.84$; $P = 0.003$). Young sows stood significantly less, than mid parity ($P = 0.008$) and old sows ($P = 0.036$), for which the relative frequency of standing did not differ ($P = 0.840$; Young: 0.16 ± 0.03 , Mid: 0.24 ± 0.03 , Old: 0.25 ± 0.04 , mean relative frequency \pm SEM). Sows stood less in late gestation than in early ($P = 0.001$) and mid gestation ($P = 0.051$), and for sows in early and mid gestation the relative frequency of standing did not differ ($P = 0.112$; Early: 0.28 ± 0.03 , Mid: 0.21 ± 0.03 , Late: 0.16 ± 0.03 , mean relative frequency \pm SEM). There was no interactive effect of treatment and stage of gestation on the relative frequency of standing in PM (Table C.1).

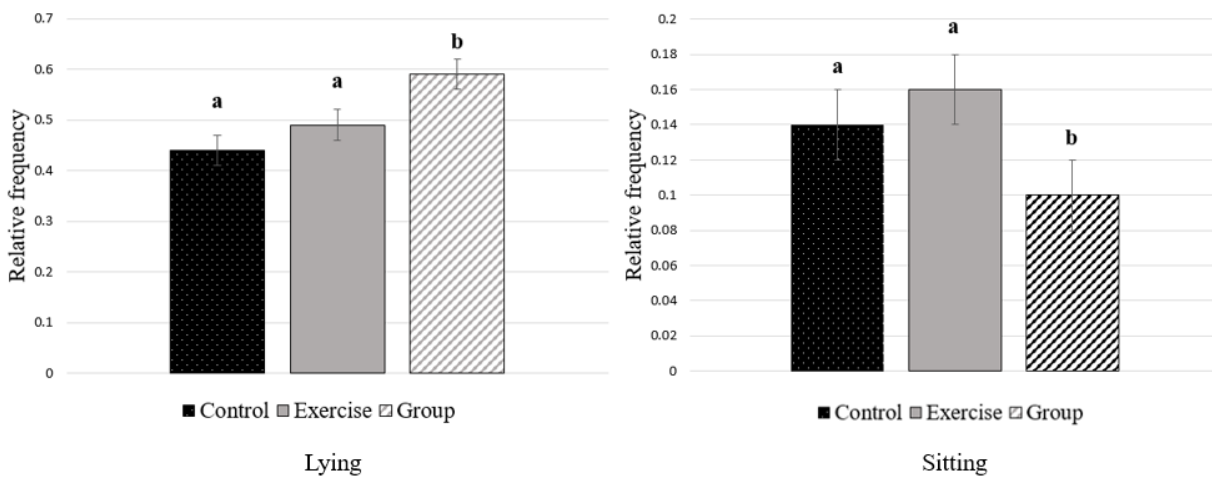


Fig. 5.2. Relative frequency (mean \pm SEM) of lying (left) and sitting (right) during the AM data collection period for sows stall-housed throughout the gestation (Control, $n = 53$), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, $n = 56$) and sows housed in groups from insemination to farrowing (Group, $n = 58$). The non-transformed (raw) mean and SEM values are presented. Where superscripts differ, $P \leq 0.05$.

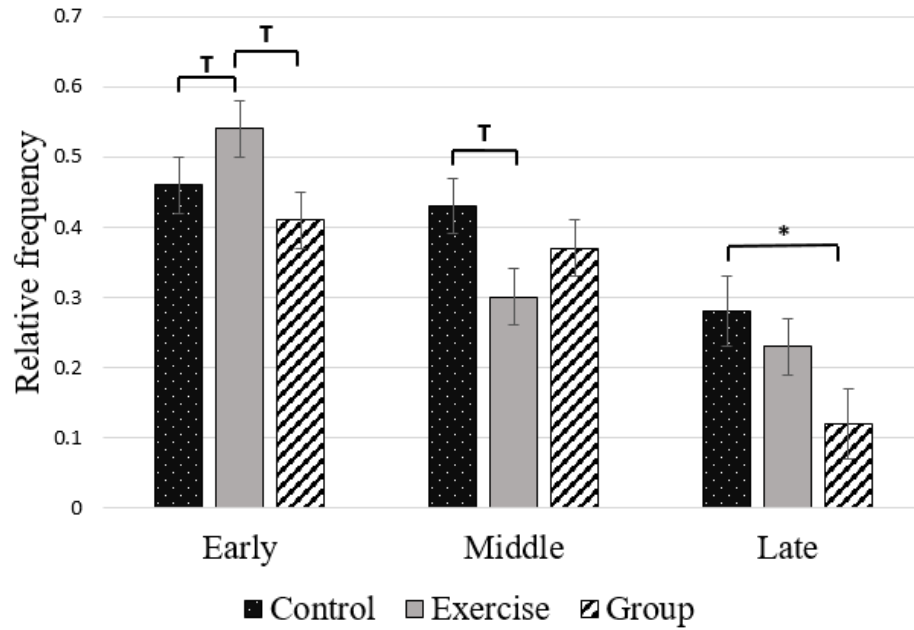


Fig. 5.3. Relative frequency (mean \pm SEM) of standing during the AM data collection period for sows stall-housed throughout the gestation (Control, $n = 53$), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, $n = 56$) and sows housed in groups from insemination to farrowing (Group, $n = 58$) in early (week 2), mid (week 10) and late gestation (week 15). The non-transformed (raw) mean and SEM values are presented. Brackets connect treatments with significant differences.* $P \leq 0.05$; T: Tendency, $P < 0.1$.

5.3.1.2 Stereotypic behaviour

There was an interactive effect of treatment and stage of gestation on the relative frequency of stereotypies in AM ($F_{4,456} = 2.51$; $P = 0.041$). Control sows in early gestation tended to perform more stereotypies than G sows, but did not differ from E sows, which performed significantly more stereotypies than G sows. In mid gestation, G sows performed fewer stereotypies than C and E sows, which did not differ. However, in late gestation, the relative frequency of performing stereotypies did not differ across all three treatments (Fig. 5.4). Control sows in early gestation performed fewer stereotypies than in mid ($P < 0.001$) and late gestation ($P = 0.019$), which did not differ ($P = 0.223$). Similarly, E sows in early gestation performed fewer stereotypies than in mid ($P = 0.001$) and late gestation ($P = 0.017$), which did not differ ($P = 0.447$). Sows from the group treatment in late gestation performed significantly more

stereotypies than in early ($P < 0.001$) and mid gestation ($P = 0.005$), for which the relative frequency of performing stereotypies did not differ ($P = 0.221$).

There was also an interactive effect of treatment and parity group on the relative frequency of performing stereotypies in AM ($F_{4,446} = 3.06$; $P = 0.017$). Young C sows performed more stereotypies than young E ($P = 0.016$) and G sows ($P = 0.005$), which did not differ ($P = 0.895$). Mid parity E sows performed more stereotypies than mid C ($P = 0.019$) and G sows ($P < 0.001$), which did not differ ($P = 0.231$). Old G sows performed fewer stereotypies than old C ($P = 0.035$) and E sows ($P = 0.020$), which did not differ ($P = 0.739$). Young C sows performed fewer stereotypies in AM, than old control sows ($P = 0.003$), and they tended ($P = 0.058$) to perform fewer stereotypies than mid parity C sows. Mid C sows tended ($P = 0.089$) to perform fewer stereotypies than old C sows. Young E sows performed significantly fewer stereotypies than mid ($P < 0.001$) and old E sows ($P < 0.001$), which did not differ ($P = 0.614$). Similarly, young G sows performed fewer stereotypies, than mid parity ($P < 0.001$) and old ($P = 0.012$) G sows, which did not differ ($P = 0.768$; Young C: 0.58 ± 0.04 , Mid C: 0.67 ± 0.03 , Old C: 0.77 ± 0.05 ; Young E: 0.41 ± 0.05 , Mid E: 0.77 ± 0.03 , Old E: 0.78 ± 0.06 ; Young G: 0.41 ± 0.04 , Mid G: 0.60 ± 0.03 , Old G: 0.59 ± 0.06 , mean relative frequency \pm SEM).

In PM, the relative frequency of performing stereotypies was influenced by the stage of gestation ($F_{4,446} = 3.06$; $P = 0.006$). In mid gestation, sows performed more stereotypies, than in early ($P = 0.005$) and late gestation ($P = 0.007$), for which the levels of performing stereotypies did not differ ($P = 0.936$; Early: 0.30 ± 0.03 , Middle: 0.43 ± 0.03 , Late: 0.34 ± 0.03). There was no interactive effect of treatment and stage of gestation on the relative frequency of performing stereotypies in PM (Table C.3).

There was an interactive effect of treatment and parity group on the relative frequency of performing stereotypies in PM ($F_{4,471} = 4.47$; $P = 0.002$). Young C sows performed more stereotypies than young E sows ($P = 0.007$), and they tended to perform more stereotypies than young G sows ($P = 0.067$). Young E sows did not differ in their levels of performing stereotypies from young G sows ($P = 0.288$). Mid parity G sows performed fewer stereotypies than mid C ($P = 0.004$) and E sows ($P < 0.001$), which did not differ ($P = 0.283$). Old E sows performed more stereotypies, than old C sows ($P = 0.017$), and they tended to perform more stereotypies than old G sows ($P = 0.054$), but the relative frequencies of performing stereotypies in old C and old G sows did not differ ($P = 0.822$). Young C sows did not differ in their performance of stereotypies

from mid ($P = 0.455$) and old C sows ($P = 0.266$), but mid control sows tended ($P = 0.067$) to perform more stereotypies than old C sows. Young E sows performed fewer stereotypies, than mid ($P < 0.001$) and old exercised sows ($P < 0.001$), which did not differ ($P = 0.641$). For G sows, the levels of performing stereotypies did not differ across different parity groups (Young G vs Mid G: $P = 0.749$, Mid G vs Old G: $P = 0.703$, Young G vs Old G: $P = 0.577$; Young C: 0.39 ± 0.05 , Mid C: 0.44 ± 0.04 , Old C: 0.32 ± 0.07 ; Young E: 0.19 ± 0.06 , Mid E: 0.49 ± 0.04 , Old E: 0.54 ± 0.07 ; Young G: 0.27 ± 0.05 , Mid G: 0.29 ± 0.04 , Old G: 0.32 ± 0.08 , mean relative frequency \pm SEM).

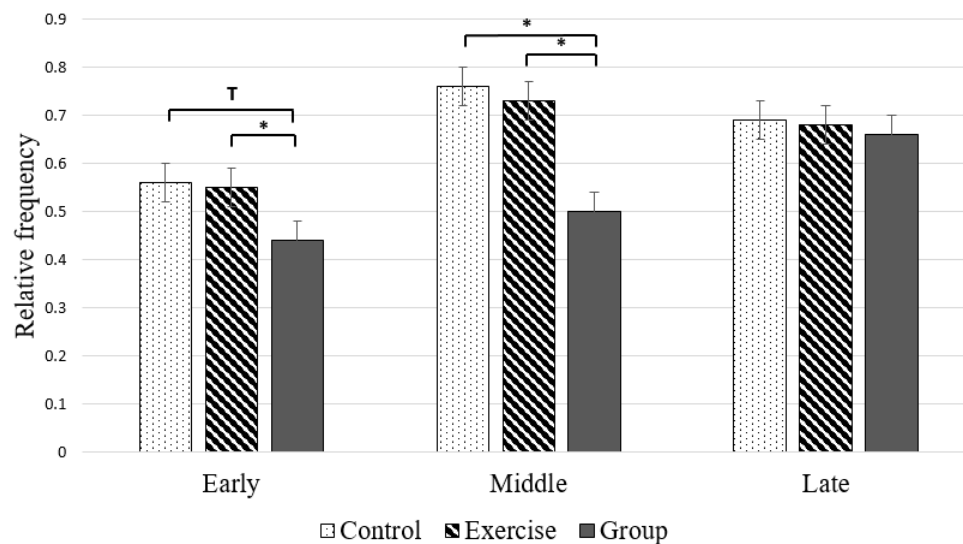


Fig. 5.4. Relative frequency (mean \pm SEM) of performing stereotypies (a total of sham chewing, bar-biting, tongue-rolling and trough manipulation) during the AM data collection period for sows stall-housed throughout the gestation (Control, $n = 53$), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, $n = 56$) and sows housed in groups from insemination to farrowing (Group, $n = 58$) in early (week 2), mid (week 10) and late gestation (week 15). The non-transformed (raw) mean and SEM values are presented. Brackets connect treatments with significant differences. * $P \leq 0.05$; T: Tendency, $P < 0.1$.

5.3.2 Hair cortisol analysis

The intra-assay coefficients of variation for high and low hair concentration samples were 6.37% and 13.75%, respectively. The inter-assay coefficients of variation for high and low cortisol concentration were 13.82% and 7.06%, respectively. The coefficients of variation between duplicate samples were not higher than the accepted cut-offs (15%). However, the final results need to be interpreted with caution, as some of the intra-assay coefficients of variation were higher than the accepted cut-off of 10%, which might reflect some pipetting errors for example.

There was no effect of treatment on sow hair cortisol levels (C: 37.24 ± 5.81 pg/mg; E: 29.34 ± 5.41 pg/mg; G: 35.83 ± 5.41 pg/mg; $F_{2,53} = 0.91$; $P = 0.410$).

5.3.3 Piglet behavioural response to stress tests

During the isolation test, piglets from C and G sows had a tendency to vocalize more, than piglets from E sows (Table 5.2), with the numbers of vocalizations from piglets of C and G sows being no different.

During the novel object test, piglets from C sows visited significantly more squares, than piglets from E and G sows which did not differ (Table 5.2). Piglets from C sows also had a tendency come within 0.50 m of the novel object more frequently than piglets from E sows, with piglets from G sows being intermediate.

All other results of the isolation test and the novel object test did not differ across treatments (Table 5.2).

In the novel object test, the latency to enter the 1.00 m circle tended to be influenced by parity group ($F_{2,112} = 2.41$; $P = 0.095$): piglets from old parity sows tended to have lower latency to enter the 1.00 m circle, than piglets from young and mid parity sows, which did not differ (Young (n = 14): 39.76 ± 8.45 , Mid (n = 34): 41.66 ± 5.65 , Old (n = 9): 28.41 ± 9.64 , mean latency (s) \pm SEM). All other results of the novel object test did not differ across parity groups (Table C.4).

Table 5.2. Results of isolation and novel object tests in piglets (n = 168, 3 piglets per sow from 54 sows and 2 piglets per sow from 3 sows), born from sows stall-housed throughout the gestation (Control, n = 17), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, n = 20) and sows housed in groups from insemination to farrowing (Group, n = 20), mean \pm SEM. The non-transformed (raw) mean and SEM values are presented. The values with different superscript letters are significantly different ($P \leq 0.05$), asterisks indicate tendency ($P < 0.1$).

Variable	Control (n = 49)		Exercise (n = 59)		Group (n = 60)		F- value	P- value
	Mean	SEM	Mean	SEM	Mean	SEM		
<i>Isolation test</i>								
Number of squares visited	23.52	2.28	18.31	2.10	19.18	2.09	1.63	0.199
Number of vocalizations	80.51 ^{a*}	7.32	65.14 ^{b*}	6.92	78.70 ^{a*}	6.89	3.02	0.052
<i>Novel object test</i>								
Number of squares visited	23.10 ^a	2.21	17.64 ^b	2.17	18.67 ^b	2.16	3.14	0.046
Number of vocalizations	61.05	7.09	48.41	7.00	57.12	6.97	1.55	0.216
Frequency of entering the 1.00 m circle	4.99	0.48	4.03	0.47	4.23	0.47	1.65	0.196
Frequency of entering the 0.50 m circle	2.64 ^{a*}	0.28	1.86 ^{b*}	0.27	2.01 ^{ab*}	0.27	2.94	0.056
Frequency of exiting the 1.00 m circle and remaining in the area bordering the perimeter of the pen	2.45	0.27	1.98	0.27	2.27	0.24	0.98	0.379
Latency to enter the 1.00 m circle (s)	30.54	7.33	41.78	7.19	37.51	7.15	0.50	0.606
Latency to enter the 0.50 m circle (s)	40.95	7.91	56.53	7.79	47.13	7.75	0.40	0.670
Latency to touch the novel object (s)	45.03	7.92	61.67	7.80	51.33	7.77	0.47	0.623
Number of contacts with the novel object	3.21	0.48	2.32	0.47	2.19	0.47	0.92	0.400

5.4 Discussion

In the present study, the effects of providing periodic exercise to gestating stall-housed sows on sow behaviour, sow hair cortisol concentration and piglet behavioural response to stress tests were investigated. The analysis of postures showed that G sows laid more (in AM) and sat less (in AM and PM) than stall-housed sows with or without access to periodic exercise. Also, G sows stood less in AM in late gestation than C sows. These results are in agreement with findings of Weng et al. (2009) and Chapinal et al. (2010), who reported a greater proportion of lying in sows housed in groups, than in stall-housed sows. Weng et al. (2009) also reported that stalled sows spent more time sitting and standing than group-housed sows. If the increased proportion of standing is interpreted as being more restless, and the increased proportion of lying is interpreted as being less restless, then the sows which were standing more may be considered as having lower welfare due to being more prone to stress as indicated by increased restlessness, than those sows which were lying more. Previous research has shown that sows that show lower activity when housed in tether stalls and groups have a higher density of mu opioid receptors in the frontal cortex, which suggests that in chronic stress situation these animals would have higher levels of circulating endogenous opioids, diminishing the impact of stress (Zanella et al., 1996; Drolet et al., 2001). Odberg (1987) demonstrated that frustration, induced by unresolved conflicts (such as an unsatisfied need for exploration in animals housed in the barren environment) can elevate the levels of arousal and lead to increased general activity, which could also explain the higher relative frequency of standing. At the same time, the type of housing system and space allowance need to be considered when interpreting these results. For instance, the increased proportion of time spent lying at cost of reduced time spent standing can be observed in sows housed in narrow stalls, which suggests that severe space restrictions increase the difficulty of standing (Li and Gonyou, 2007). Sitting, as intermediate posture between lying and standing, is suggested to be an indicator of difficulty to change posture, for example in a narrow stall (Li and Gonyou, 2007), which can explain the decrease in the relative frequency of sitting in group-housed sows. In the current study, the lower performance of lying behaviour and increased performance of standing in stall-housed (control and exercised) sows is possibly linked to lower levels of lying comfort and increased restlessness in these animals. Restlessness could be induced by frustration related to prevention of foraging in feed-restricted sows, which is highly motivated behaviour (Odberg, 1978), especially in the presence of feed trough in the stall.

This idea is supported by the fact that the majority of the posture differences were observed in AM, in the hours following the sows finishing their meal. Reduced level of comfort in the stall (due to restricted space and lack of control over the environment, such as inability to separate dunging, feeding and lying areas, inability to adjust the location in response to ambient temperature, lack of opportunities to establish a social relationship and inability to avoid aggressive sows or fear eliciting stimuli) has been proposed to reduce the relative frequency of lying in stalled sows (Rhodes et al., 2005).

C and E sows did not differ in their relative frequency of lying and sitting, and also standing in late gestation, as opposed to the study of Harris et al. (2013), which found that stall-housed gilts sat longer, stood less, and tended to lie more in comparison to exercised gilts. This difference might be due to the more intensive exercise schedule used in the study of Harris et al. (2013), which required gilts to be exercised for 30 mins three times per week from mid to late gestation. Exercising sows at the level of intensity used by Harris et al. (2013) could contribute to an increase in sow bone density, as demonstrated by Schenck et al. (2008), who also used high-intensity periodic exercise schedules, which would explain the increased ease and hence higher duration of standing in exercised animals. This finding suggests that periodic exercise provided at a low level, proposed in the current study, does not influence the sow postural repertoire compared to animals housed in groups. On this basis, it could be expected that this low level of exercise does not affect sow bone density.

The relatively small body size of young sows, which allows fitting in conventional stalls more comfortably, and perhaps a lower level of frustration (which could be a cumulative effect of confinement over consecutive gestations in older sows) may explain the increased relative frequency of lying in AM, decreased relative frequency of standing in AM and PM, as well as a tendency to the increased relative frequency of lying in PM in the young parity sows. These results are in agreement with the findings of Broom et al. (1995), who reported an increase in general activity (as determined by the time spent in standing, sitting and moving) in fourth parity sows in comparison to first parity sows in stalls and groups, with the most dramatic increase being observed in stall-housed sows. Similarly, Zhang et al. (2017) found that stall-housed pregnant gilts (starting from day 55 of gestation) stood less than parity 3-4 sows and that parity 0-1 sows lay laterally more than older sows (parity 2 and 5), suggesting that younger and smaller

animals experience more comfort in standard stalls due to a proportionally lower space restriction, than older and larger sows.

The increase in the relative frequency of lying (in AM and PM) and sitting (in AM) and decrease in the relative frequency of standing in AM and PM as gestation advanced, is consistent with previous literature. For example, Marchant-Forde and Marchant-Forde (2004) reported a progressive decline in the proportion of observations spent standing and a corresponding increase in lying behaviour (from 54% to 73% of the time) over gestation in group-housed gilts. These results could be related to an increase in metabolic requirements and weight of actively growing fetuses, which promotes a reduction in physical activity. The observed shift in activity levels also could happen due to the changes of sow size, with larger sows during the advanced stages of gestation finding it more difficult to move (especially if housed in stalls).

It was found that in early and mid gestation G sows performed fewer stereotypies in AM compared to stall-housed sows (with or without having opportunities to exercise periodically), but for late gestation in AM, and for all stages of gestation in PM the levels of performing stereotypies did not differ across treatments. The AM results suggest that housing in barren group pens can temporarily relieve stress, related primarily to frustration post feeding due to ingestion of an insufficient amount of feed (Chapinal et al., 2010) during the first two trimesters of sow gestation, but it is not effective during the last trimester of pregnancy. No differences in performing stereotypies in PM suggest that group housing does not reduce the performance of stereotypies which are not associated with restricted feeding.

Interestingly, the performance of stereotypies in AM in sows from all treatments increased with age and with the stage of gestation. These findings are in agreement with the results of Broom et al. (1995), who reported that fourth parity sows had a higher proportion of time spent in sham-chewing, in comparison to primiparous sows. Zhang et al. (2017) also reported the results, comparable to the current study: the authors demonstrated a gradual increase in the frequency of sham-chewing from day 25 to day 100 of gestation in stall-housed sows, and a significantly higher frequency of sham-chewing in parity 5 sows, in comparison to younger sows. Both of these effects may be due to a cumulative effect of confinement in stall-housed sows (Zhang et al., 2017), and hence sows that experience the longest confinement durations (old animals and animals in the last trimester of gestation) could have a higher incidence of stereotypies in comparison to the sows, which were confined for a shorter period of time. For the

group-housed sows, the increase in performance of stereotypies may be due to a cumulative effect of stress experienced by sows in groups, possibly because of the lack of opportunities to express the full repertoire of innate behaviours, such as rooting and nest-building, in the barren pen environment, and also due to social stress related to an inability to avoid aggressive pen mates and competition over preferred lying areas (Spooler and Vermeer 2015). The increase in performing stereotypies in older sows can also be related to bigger stomach size in large animals. Being feed-restricted in these sows results in lower gut fill, which leads to increased feeding motivation (Holt et al., 2006), developing higher levels of frustration and performing more stereotypies in response to this frustration, in comparison to younger sows that have smaller stomach size.

The present study showed that young and old G sows performed fewer stereotypies than both C and E young sows, and mid parity G sows performed fewer stereotypies than E sows in AM. Similarly, in PM young G sows tended to perform fewer stereotypies than C sows, mid parity sows from the group treatment performed fewer stereotypies than stall-housed sows (with or without access to periodic exercise), and old G sows tended to perform fewer stereotypies than E sows. These results demonstrate a general trend of reduction in performing stereotypies in group-housing settings by the sows of all ages. These findings are in agreement with the results of Broom et al. (1995) and Chapinal et al. (2010), who demonstrated that stall-housed sows had a higher level of performing stereotypies than sows in group-housing systems. Given that the development of stereotypies is promoted by the lack of opportunities to exhibit a full repertoire of animals' innate behaviours (Fraser et al., 1997) and their presence is considered to be an indicator of stress, it can be concluded that G sows in the current study experienced lower levels of stress in comparison to stall-housed animals, and providing periodic exercise to stall-housed sows did not help to reduce this stress.

In the current study, sow hair cortisol was measured to assess the levels of chronic stress, experienced by pregnant sows during gestation. The obtained values of hair cortisol concentration are within the previously reported range for gestating sows (Bacci et al., 2014; Roelofs et al., 2019; Everding et al., 2020). Hair cortisol concentrations were not affected by sow treatment, which implies that the levels of sow chronic stress did not depend on the level of access to a greater freedom of movement. In contrast, Everding et al. (2020) demonstrated that stall-housed sows had higher hair cortisol levels over gestation than sows housed in groups of

10-15 sows. The rapid rise of cortisol levels during the third trimester of pregnancy is more a physiological response of an organism to impending labour (Dorr et al., 1989) than an indicator of stress, caused by restricted freedom of movement, and theoretically, this preparturient increase in cortisol concentration could even out the differences between treatments in the current study. However, the differences in group space allowance, number of animals in the group, feeding system, group pen design and flooring could be the factors that contributed to detectably decreased levels of hair cortisol in group-housed sows in the study of Everding et al. (2020). This idea is further supported by the discrepancy in the hair cortisol and stereotypy data from the current study, as the analysis of stereotypies suggests that G sows performed fewer stereotypies than stall-housed sows (with or without access to periodic exercise), and hence they were less stressed.

The current study demonstrated rather ambiguous effects of providing a greater freedom of movement to the sow on the piglet behavioural response to stress tests. In a social isolation test, the number of visited squares did not differ across treatments. This result is in agreement with the study of Brajon et al. (2017), in which piglets from group-housed sows exposed to the social stress of mixing in mid gestation and from non-stressed group-housed sows did not differ in the number of squares visited. The authors of the latter study suggest that the stress due to social isolation could be stronger than prenatal stress, and hence the differences caused by prenatal stress could have been masked.

The number of vocalizations in the social isolation test was higher in piglets from C and G sows than in piglets from E sows. Similarly, Sorrells et al. (2006) demonstrated that the frequency of squealing during the isolation test did not differ between piglets from stall-housed and group-housed sows; however, piglets from stall-housed sows grunted more than piglets from the sows, group-housed throughout gestation. In contrast, Brajon et al. (2017) reported that piglets from group-housed sows exposed to social stress of mixing in mid gestation had a lower frequency of low calls in comparison to piglets from non-stressed sows; however, prenatally stressed piglets did not differ in the total number of vocalizations from piglets of non-stressed group-housed sows. Considering that grunting may be interpreted rather as an indicator of exploration than as a sign of stress (Sorrells et al., 2006), it can be assumed that piglets from non-stressed sows in the latter study performed more exploration than piglets from socially stressed sows. Hence, the previous literature suggests that being exposed to prenatal stress may

affect the number of vocalizations in the social isolation test. However, the amplitude of sound should be taken into account, and in the current study only the number of vocalizations was recorded. Based on the presented results it can be concluded that piglets from stall-housed throughout gestation and group-housed sows may experience similar levels of prenatal stress, and providing periodic exercise to stall-housed sows may relieve the effects of this stress; however, for better understanding of the levels of stress experienced by piglets from different treatments, a separate analysis of vocalizations of low and high amplitude might be needed.

In the novel object test, piglets from C sows visited more squares in comparison to piglets from E and G sows and tended to have the higher number of times spent in close proximity to the novel object (0.50 m), which in previous literature was interpreted as an indicator of lower anxiety in these piglets (Kranendonk et al., 2007). However, in the current experimental conditions it was noticed, that in those piglets that had increased locomotor activity, the patterns of movement were fairly chaotic and they were avoiding touching the novel object, suggesting that these animals were rather fearful of it. A similar explanation may be applied to the higher number of times spent near the novel object in piglets from C sows, which may be a result of increased activity due to anxiety and hence higher frequency of sporadic approaches to the novel object. Weaver et al. (2000) found that boars neonatally stressed by handling for the first 14 days of life entered more inner squares of the pen in an open field test at 7 months of age in comparison to non-stressed boars. The authors reported that it was not a reflection of increased activity, as the number of visited outer squares was reduced proportionally; therefore, it was concluded that this alteration in behaviour supposedly indicates reduced anxiety levels in neonatally stressed boars. However, unlike in the study of Weaver et al. (2000), in the current study the levels of activity were increased when the novel object, which probably was the main source of anxiety, was present in the testing arena. These discrepancies suggest that piglets from C sows in the current study were more active due to being more anxious.

Interestingly, in the current experiment the results of the novel object test did not differ for piglets from sows, receiving some exercise during gestation (E and G sows), while being different for piglets from C sows. This suggests that providing a greater freedom of movement may positively affect piglet behavioural response to stress, considering that exercised sows were more adapted to 'life changes' than sows which were restrained in stalls throughout gestation.

Such variables as the number of vocalizations and the number of contacts with the novel object in the novel object test did not differ across treatments, suggesting that these variables were not influenced by the maternal level of access to a greater freedom of movement. These results are in agreement with the study of Kranendonk et al. (2006), who found no difference in these parameters between piglets from control and prenatally stressed sows. However, Kranendonk et al. (2006) used oral administration of hydrocortisone-acetate as opposed to the naturally induced stress, applied in the current study. Responses to these stressors cannot be compared accurately due to the difference in physiological changes, and also due to exposing animals to additional stress during the hormone administration (Lay et al., 2008). On the other hand, similarly to the isolation test, the stress caused by the novel object test could have been masking more subtle effects of prenatal stress. In contrast, Tatemoto et al. (2019) found that female piglets born from sows that had access to straw during pregnancy, spent more time interacting with the novel object than female piglets from sows housed in the barren environment throughout gestation, which suggests that piglets from sows having access to environmental enrichment were less fearful. However, the piglets used in the study of Tatemoto et al. (2019) were tested at 41 days of age, whereas piglets from the current study were tested on day 19-22 of age. This implies that the effects of prenatal stress on piglet behavioural response to stress tests may be developing with a delay.

The latency to touch the novel object did not differ across treatments in the current study. In contrast, Kranendonk et al. (2007) found that piglets from the sows with a high social rank, which presumably experienced lower levels of stress during gestation, had a lower latency to touch the novel object, in comparison to the sows that had a low social rank. These results suggest that for sows, being housed in a confined barren environment or small groups of four (as in the current study) may lead to lower levels of gestational stress in comparison to being housed in large groups, if it involves experiencing aggression of dominant pen mates during gestation, and hence piglets from stall-housed or group-housed (in small groups) sows may be less prenatally stressed than piglets from subordinate sows, housed in larger groups of 7-14 sows, as described by Kranendonk et al. (2007).

5.5 Conclusions

Providing periodic exercise to stall-housed gestating sows at low levels used in the current study did not improve sow comfort, as indicated by similar relative frequencies of standing, sitting and lying in stall-housed throughout gestation and periodically exercised sows. Similarly, the relative frequencies of performing stereotypies by periodically exercised sows were comparable to those recorded in sows, stall-housed throughout gestation. However, housing in groups was shown to improve sow comfort and reduce the performance of stereotypies in comparison to stall-housed sows (with or without access to periodic exercise), which is considered to be linked to lower levels of gestational stress in group-housed sows. Sow hair cortisol analysis was unable to identify the difference in the levels of chronic stress experienced by pregnant sows with different levels of access to a greater freedom of movement, possibly due to taking an approach of measuring average cortisol levels for the whole gestation cycle, which needs to be considered. In piglets, the results of behavioural testing demonstrated the effect of sow treatment on the piglet behavioural response. In particular, the novel object test indicated that the lack of access to greater freedom of movement in stall-housed sows resulted in more proactive behavioural response in offspring.

The finding of this study supports the idea that providing a greater freedom of movement can bring some welfare benefits to the sow, and implies that group housing appears to be the most effective way of providing a greater freedom of movement to stall-housed gestating sows. However, to achieve the optimal levels of animal welfare, a complex approach including not only providing a greater freedom of movement, but also other methods of enhancing sow welfare, such as fulfilling exploratory and feeding motivations, need to be used. Sow gestation housing was found to influence offspring characteristics, which should be studied in greater depth as producers make the transition to group housing and new farming and husbandry methods are being developed globally.

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6. THE EFFECT OF PROVIDING A GREATER FREEDOM OF MOVEMENT THROUGH PERIODIC EXERCISE ON REPRODUCTIVE PERFORMANCE, PLACENTAL CHARACTERISTICS AND PIGLET VIABILITY IN STALL-HOUSED GESTATING SOWS

The results presented in Chapters 3 and 4 demonstrated that stall-housed gestating sows are motivated to exit their stalls, and the finding presented in Chapter 5 revealed that low levels of periodic exercise in gestating sows can alter piglet behavioural response to behavioural stress tests. However, providing periodic exercise to gestating sows housed in commercial barns could result in significant costs through additional labour. These costs could be offset by improving sow productivity, and therefore whether periodic exercise can influence sow reproductive performance needs to be studied. Additionally, the physiological mechanisms by which periodic exercise could improve sow productivity need to be revealed. In Chapter 6, the effects of periodic exercise on sow reproductive performance, placental characteristics and piglet viability were presented and compared to those observed in stall-housed sows receiving no exercise and group-housed sows. The results show that periodic exercise benefited the reproductive performance in older parity sows, increasing liveborn.

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Abstract

The 2014 Canadian Pig Code of Practice included a recommendation to provide stall-housed gestating female pigs with periodic exercise. The effects of periodic exercise on sow reproductive performance, placental and piglet characteristics were determined. Sows ($n = 180$) were assigned to one of three gestation treatments: stall-housed sows (Control: C), stall-housed sows given weekly exercise (Exercise: E – walking for 160 m), group-housed sows (Group: G). Sows belonged to one of three parity groups: young (parity 0-1), mid (parity 2-4), old (parity 5-7). Sow reproductive performance, placental characteristics and piglet viability were recorded at farrowing. Old C sows had larger litters than G sows, and E sows were intermediate; mid G sows had larger litters than E and C sows, which did not differ ($P = 0.023$). Old E and G sows did not differ in total liveborn piglets, and both had a greater number of liveborn than C sows ($P = 0.033$). Piglets from old C sows had a greater latency to reach the teat than E and G piglets, which did not differ ($P = 0.010$). Periodic exercise benefited the reproductive performance and piglet viability in older parity sows, increasing liveborn and reducing piglet latency to reach the teat.

Key words: gestation stall, gestational stress, periodic exercise, pig, placenta, reproductive performance.

6.1 Introduction

To address a strong societal concern about physical and social restrictions experienced by stall-housed gestating sows, the recommendation to provide gestating female pigs with more freedom of movement as of 2024 was included in the 2014 Code of Practice for the Care and Handling of Pigs (NFACC, 2014). The Code states that meeting this recommendation should be achieved by implementing group housing system in all newly built barns, and by providing sows housed in stall barns built prior to 2014, which are in good working order, with opportunities for a greater freedom of movement, such as periodic exercise. Previous research has shown that stall-housed gestating female pigs are motivated to exit their stall (Chapter 3), and also that low levels of periodic exercise in gestating sows can alter piglet behavioural response to behavioural stress tests (Chapter 5). However, exercising sows in commercial barns could result in significant costs for the industry through additional labour, as sows would need to be exercised one at a time to prevent aggressive interactions. Periodic exercise could be a more viable option of providing a

greater freedom of movement if the costs of exercising could be offset by improving sow productivity. Earlier studies identified that intensive exercise regimes impact sow reproductive physiology through changes in umbilical blood flow (Harris et al., 2013) and improve sow performance by increasing piglet birth weight and reducing piglet mortality (Schenck et al., 2008), but the impact of low-level periodic exercise on sow reproductive function is unknown.

Evaluating both prenatal and postnatal piglet survival measures, which reflect the intrauterine and extrauterine environment (Baxter et al., 2008), provides a more refined approach to assessing the effects of periodic exercise on sow productivity. For example, previous research in humans suggests that most stillbirths are related to placental dysfunction, which is associated with fetal growth restriction (Smith and Fretts, 2007). Medical research also found some evidence of a positive influence of exercise on fetoplacental growth, resulting in faster placental development and improved placental function (Clapp et al., 2000). While the existing body of literature on the effects of periodic exercise on prenatal and postnatal survival in swine is limited, there is some evidence that providing a greater freedom of movement to gestating sows through housing them in groups in early gestation can improve sow conception rates and piglet prenatal survival, as demonstrated by the decreased number of stillborn piglets in sows mixed in groups after weaning in comparison to the sows mixed at five weeks post breeding (Brown, 2015). Similarly, Connor (2018) found a tendency to reduction in the number of stillborns in sows grouped at weaning, in comparison to the sows mixed into static groups within seven to eight days after weaning, and at four weeks after breeding. It was also found that housing gestating sows in groups increased chances of piglet postnatal survival, as determined by higher piglet birth weight (Bates et al., 2003). However, there is a lack of studies providing a comprehensive comparison of the measures of prenatal and postnatal piglet survival in relation to the levels of exercise, received by gestating sows, in relation to the housing system.

The objectives of this study were to determine the effects of providing periodic exercise to stall-housed sows during gestation on sow reproductive performance, placental development and piglet viability, and compare it to stall-housed sows receiving no exercise, and sows housed in groups.

6.2 Materials and methods

All experimental procedures were reviewed and approved by the University of Saskatchewan Animal Care Committee (#20170057), which is regulated by the Canadian Council of Animal Care (2009). This study was conducted at the Prairie Swine Centre, Saskatoon, Canada between February and November 2019.

6.2.1 Animals and housing

A total of 180 bred Camborough 42 sows (parities 0-7, mean parity \pm standard deviation [SD]: 2.42 ± 1.76) were studied. On day 7-10 post breeding, sows were moved from breeding stalls to free-access stall gestation pens (Egebjerg INN-O-STALL® free access stalls, Egebjerg International A/S, Nykøbing Sjælland, Denmark) and remained in the pens until day 107-110 of gestation. Each free-access stall pen contained 32 free access stalls (each 2.1 m long \times 0.65 m wide), with 16 stalls on adjacent sides of the pen, and a 3.0 m wide fully slatted loafing area in between (Rioja-Lang et al., 2013). Each free-access stall pen was divided with an opaque plastic central divider, so there were 2 lanes of 8 stalls on each side of each half of the pen. One replicate block consisted of 12 experimental animals selected within one breeding week, and a total of 15 replicate blocks were formed. For each experimental animal, body condition score (BCS) of 1 to 5 (1 = thin, 5 = fat) was recorded. Animals were fed approximately 2.2 kg of a standard sow gestation ration once daily at 0700 h, and each free access stall and central loafing area were equipped with nipple water drinkers.

Experimental sows were moved to individual farrowing crates on day 107-110 of pregnancy. The farrowing crates were equipped with electronic sow feeders (Jyga Technologies, Saint-Lambert-de-Lauzon, QC, Canada) and nipple drinkers. The farrowing rooms were illuminated by natural sunlight and artificial lightning provided between 0700 and 1500 h; on the days of farrowing data collection the artificial lightning was provided for 24 h. Farrowing was allowed to occur naturally, with limited intervention by trained personnel if a piglet birth interval was longer than 3 h, and research staff were present for data collection. A day before the expected date of farrowing, rubber mats were placed in the farrowing crates behind the sows for the purpose of collecting placentas. The mats were regularly washed and replaced with clean dry mats as needed, and were left in the crates until the end of farrowing. The piglets had access to a lit and heated area at the front of the farrowing pen, which was inaccessible to the sow. Cross-

fostering was performed within two days of age in accordance with the barn practices to maintain the litter size of 14 piglets per sow, and the numbers of piglets fostered on the sow and fostered off the sow were recorded. Husbandry procedures performed by the trained barn staff on the piglets included teeth clipping (at one day postpartum), tail docking, iron injections, ear notching and castrations (at three days of age). Weaning of piglets was performed at approximately 28 days of age.

6.2.2 Treatments

After moving to gestation pens, sows were assigned to one of three treatment groups (four sows per treatment per replicate block, $n = 180$ sows, 60 sows per treatment): sows housed in stalls throughout gestation (Control: C); stall-housed sows given weekly exercise throughout gestation (Exercise: E); sows housed in static groups of four throughout gestation (Group: G). All treatments were balanced by parity and represented within the same gestation pen. The pen design with a central divider allowed housing of two replicates within each pen. The individual sow was the experimental unit.

Sows from C treatment stayed locked in the gestation stalls during gestation. Sows from E treatment were also locked in stalls throughout gestation, but removed for exercise once a week. To provide exercise, E sows were backed out of their stalls, walked out of the gestation pen and walked in a loop twice around the alleyways surrounding half of the gestation room. Exercising was performed between 1100 and 1300 h on the same day every week. The distance walked by a sow during one exercise session was approximately 160 m. Sows were encouraged to keep moving by the handler through vocal signals, and, if needed, use of a pig board or light taps from the hand. Sows were exercised one at a time. Sows from G treatment were manually locked out of the free access stalls for 6-7 h a day, remaining in the group loafing area measuring 3.0 m by 5.35 m ($4.01 \text{ m}^2/\text{sow}$) with concrete slatted flooring, and having access to the stalls and the group area during the rest of time. Group sows were locked in the stalls once a week during the period of exercising E sows.

6.2.3 Sow performance measurements

Total litter size (a total of liveborn, stillborn and mummified piglets), as well as the numbers of live-born and stillborn piglets separately, were recorded for all sows. Body weight and crown-

rump length (the length of the piglet from the crown of the head to the base of the tail (Baxter et al., 2008)) of live-born piglets were recorded at birth. Ponderal index (PI) and body mass index (BMI) measures were adapted from Baxter et al. (2008) and determined for each live-born piglet. PI was calculated as: birth weight (kg)/(crown-rump length (m))³; BMI was calculated as birth weight (kg)/(crown-rump length (m))².

At weaning, the numbers of piglets weaned from each experimental sow were recorded, and liveborn piglet mortality percentage was calculated using an adjusted equation from the paper of Mack et al. (2014): liveborn piglet mortality (%) = ((adjusted number of live-born piglets post fostering – number of piglets weaned)/adjusted number of live-born piglets post fostering) × 100, where the adjusted number of live-born piglets post fostering was determined as: number of live-born piglets + number of piglets fostered on the sow – number of piglets fostered off the sow.

6.2.4 Placental characteristics

Placentas from 36 sows (12 sows/treatment) were collected from the rubber mats immediately upon farrowing and stored at 4 °C up to 24 h until dissection could be performed. The placentas were dissected and evaluated according to procedures adapted from the van Rens et al. (2002) and Baxter et al. (2008) techniques. Placental dissections were performed by two trained technicians: one technician was counting areolae and weighing placentas, and another technician was preparing placentas for dissection and taking all other measurements. Placentas were carefully washed, and each individual placenta was separated. The umbilical cord, necrotic tips, amnion and amniotic fluids were removed, and only the allantochorion was evaluated. Placental vascularization was evaluated macroscopically on a scale from 1 (white, fragile and thin placenta with little blood within the major blood vessels and capillaries) to 5 (deep red, thick and resistant to tearing placenta with the presence of blood within the major blood vessels and capillaries). For a full description of the placental vascularization scoring system refer to Baxter et al. (2008). The width and length of each placenta were recorded, and then the placenta was cut across its length at the anti-mesometrial side and spread out. Parts of the upper and lower allantochorion, equidistant between the centre and the edge, were placed on a board with ruler markings, and areolae, which were visible macroscopically within 5 × 5 cm quadrants on both upper (Quadrant 1) and lower (Quadrant 2) parts of allantochorion, were counted (Fig. 6.1).

Areolae were presented as white opaque circles and ellipses on the allantochorionic surface (Brambel, 1933). Afterwards, the weight of each placenta was recorded.

Placental surface area was calculated by multiplying placental width by placental length. An estimate of the total number of areolae per placenta was calculated as: (placental surface area (cm²)/total surface area of Quadrants 1 and 2 (cm²)) × total number of areolae in Quadrants 1 and 2. Areolae density was calculated as: total number of areolae per placenta/placental surface area (cm²). Placental efficiency was determined for each sow individually as average piglet birth weight (g)/average placental weight (g).

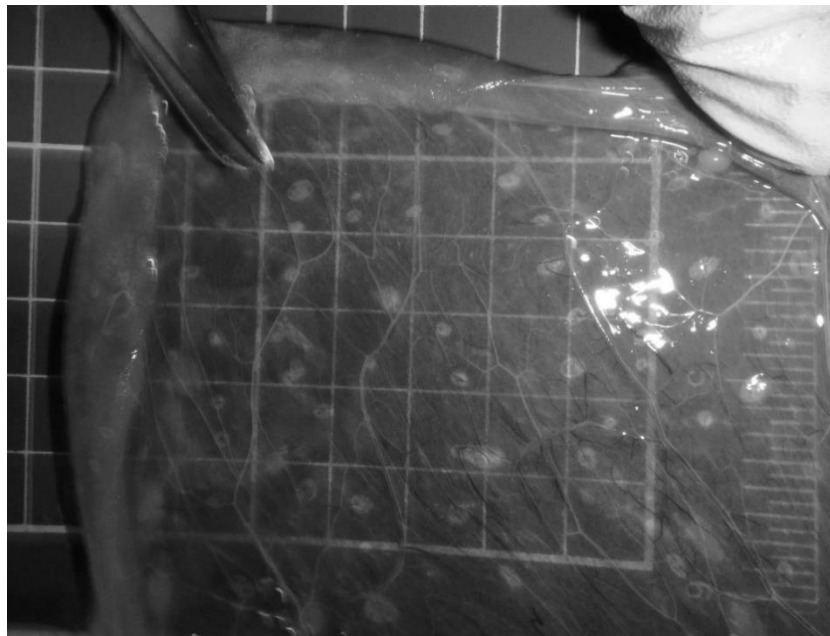


Fig. 6.1. Dissected placenta on a board with ruler markings. White opaque circles and ellipses on the allantochorionic surface represent areolae.

6.2.5 Piglet viability data collection

Sows and their piglets were continuously filmed with a camcorder (Canon Vixia HF R800, Canon Canada Inc., Brampton, ON, Canada) starting from a day before the expected date of farrowing until 3 h after the end of farrowing (when the last placenta was expelled), and after such behaviour events as standing and reaching the teat (adapted from Baxter et al., 2008) were performed by each piglet at least one time. Such piglet viability measures as farrowing duration

(the time between the birth of the first and the last piglets), farrowing duration per piglet (farrowing duration/total number of piglets born (live-born + stillborn + mummies)), latency to stand and latency to reach the teat were recorded from the video footage by one observer for 24 C sows, 27 E sows and 36 G sows. The latency to stand was defined as the time between the birth and the first successful attempt to stand, with a piglet supporting its weight on all four limbs. The latency to reach the teat was defined as the time between the birth and the piglet touching a sow's teat with its mouth for the first time. The original aim was to record farrowing from at least 36 sows per treatment, but it was impossible due to multiple camera failures.

6.2.6 Statistical analysis

For the purpose of statistical analysis, sows were assigned to one of three parity groups: young (parity 0-1), mid (parity 2-4) and old parity sows (parity 5-7). Data were analysed using the statistical package SAS 9.4 (SAS Institute, Cary, NC, USA). The significance level was set at $P < 0.05$, and results with $P < 0.10$ were considered as statistical trends. Residuals of all dependent variables were examined for normality and homogeneity of variances, and the data were transformed as necessary; the least-square means (LSMEANS) of fixed effects with Tukey's adjustment were used to account for multiple comparisons. The fit statistics of models were checked through the Akaike's information criterion corrected (AICC) and Bayesian information criterion (BIC) to ensure the best fit model was achieved. Results are presented in the mean and SEM from the raw (untransformed) data.

To compare total litter size, the number of liveborn piglets, average piglet birth weight, average piglet PI and BMI, placental surface area, areolae density, placental weight, placental efficiency, total areolae number, farrowing duration, farrowing duration per piglet, average piglet latencies to stand and to reach the teat and liveborn piglet mortality across different treatments, mixed model (PROC MIXED procedure in SAS) was used. The fixed effects of treatment, parity group, as well as the interactive effect of treatment and parity group were tested. The random effect of replicate was added to the models. Total litter size was used as a covariate in the models exploring the number of liveborn piglets, average piglet birth weight and placental efficiency, total litter size and average piglet birth weight were used as covariates in the models for placental surface area, areolae density, placental weight, total areolae number, farrowing duration and farrowing duration per piglet and adjusted number of live-born piglets post fostering was used as

a covariate in the model for liveborn piglet mortality. Farrowing duration, farrowing duration per piglet, total litter size and average piglet birth weight were used as covariates in the models for piglet latency to stand and latency to reach the teat. Collinearity between farrowing duration and farrowing duration per piglet was explored prior to inclusion in the model. The interactive effect of treatment and parity group was not significant and it was removed from the models for placental surface area, areolae density, placental weight, placental efficiency, total areolae number and liveborn piglet mortality. The total litter size, number of liveborn piglets, PI and BMI, placental surface area, placental weight, placental efficiency and total areolae number variables required square root transformation. The farrowing duration, farrowing duration per piglet, latency to stand and latency to reach the teat variables required log transformation. The liveborn piglet mortality variable was converted to the proportion and required arcsine square root transformation.

To compare the number of stillborn piglets and placental vascularization in sows across treatments, Poisson regression model (PROC GLIMMIX procedure in SAS) was used. The fixed effects of treatment, parity group and the interactive effect of treatment and parity group were tested. The random effect of replicate was added to the models. Total litter size was used as a covariate in the model for the number of stillborn piglets and total litter size and average piglet birth weight were used as covariates in the model for placenta vascularization. The interactive effect of treatment and parity group was not significant and it was removed from the model for placental vascularization.

6.3 Results

In total, 11 sows were removed from the trial and their data were not included in the final analysis: three of these sows were removed due to illness (two control and one group sow), and eight sows aborted (five control, two exercise and one group sow). Additionally, piglets for which the farrowing assistance was required, were excluded from the piglet viability analysis, and sows which required farrowing assistance were not included in the farrowing duration data. For the main effects, P-values and F-values are discussed, and adjusted P-values are presented for post hoc comparisons.

6.3.1 Sow performance

There was an interactive effect of sow treatment and parity group on total litter size ($F_{4,156} = 2.92$, $P = 0.023$) and the number of liveborn piglets ($F_{4,155} = 2.70$, $P = 0.033$). Gestation treatment predominantly influenced the performance of older parity sows: old parity C sows had larger litters than G sows, and E sows were intermediate (Fig. 6.2). Within mid parity sows: G sows had larger litters, than both E and C sows, which did not differ (Fig. 6.2). Old C sows had higher total litter size than young ($P = 0.001$) and mid C sows ($P = 0.026$); young C sows tended ($P = 0.088$) to have lower total litter size than mid C sows. Mid E sows tended ($P = 0.061$) to have lower litter size than old E sows, with young E sows being no different from mid and old E sows. Young G sows had significantly lower ($P = 0.002$) total litter size than mid G sows, with old G sows being intermediate. Old C sows had a lower number of liveborn piglets than old E sows, and they tended to have a lower number of liveborn piglets than old G sows, but old E and G sows did not differ in total liveborn piglets (Fig. 6.3). Old C sows had a significantly lower number of liveborn piglets than young ($P = 0.002$) and mid C sows ($P = 0.008$), which were no different. There were no other treatment and parity group interactions on the total litter size and number of liveborn piglets.

The interaction of treatment and parity group tended ($F_{4,158} = 2.22$, $P = 0.069$) to affect the number of stillborn piglets. Old parity C sows had more stillborns than E sows ($P = 0.013$), with G sows being intermediate. However, given that the main effect of the model showed only a tendency, the difference between old parity C sows and old parity E sows was also interpreted as a tendency (Fig. 6.4). Old C sows tended to have more stillborn piglets than young and mid C sows, which did not differ. There were no other treatment and parity group interactions on the number of stillborn piglets.

There was no effect of treatment or interactive effect of treatment and parity group on piglet birth weight. However, sow parity group influenced piglet birth weight: mid parity sows had significantly heavier piglets than young and old parity sows, which did not differ (Young: 1.43 ± 0.03 , Mid: 1.51 ± 0.03 , Old: 1.38 ± 0.04 ; mean \pm SEM, kg; $F_{2,157} = 5.21$, $P = 0.007$).

There was no effect of treatment (Table 6.1) on PI, BMI and liveborn piglet mortality, as well as no effect of parity group and no interactive effect of treatment and parity group on PI and BMI. Parity group tended to affect liveborn piglet mortality, with sows from the old parity group tending to have higher piglet mortality proportion than young and mid sows, which did not differ (Young: 0.11 ± 0.02 , Mid: 0.11 ± 0.01 , Old: 0.15 ± 0.03 ; mean \pm SEM; $F_{2,159} = 2.45$, $P = 0.089$).

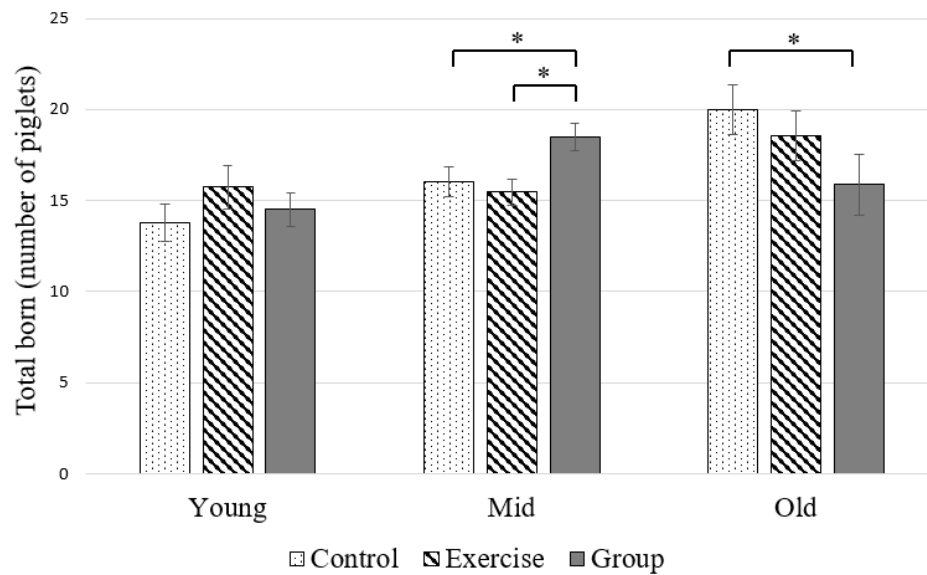


Fig. 6.2. Total born (mean number of piglets \pm SEM) for sows, stall-housed throughout the gestation (Control, $n = 53$), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, $n = 56$) and sows housed in groups from insemination to farrowing (Group, $n = 58$), belonging to young (parity 0-1; $n = 49$), mid (parity 2-4, $n = 95$), and old (parity 5-7, $n = 24$) parity groups. The non-transformed (raw) mean and SEM values are presented. Brackets connect treatments with significant differences, * $P < 0.05$.

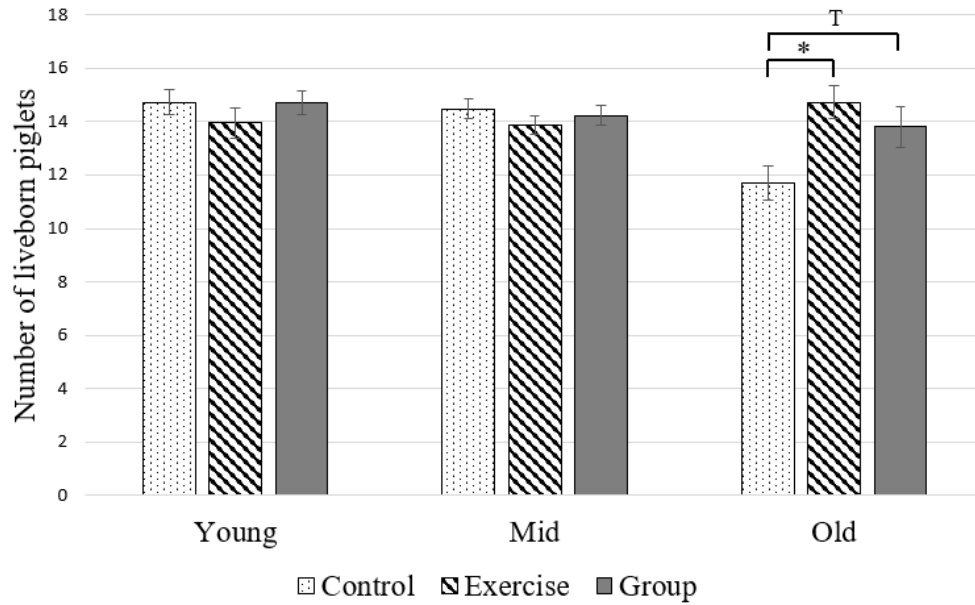


Fig. 6.3. Number of liveborn piglets (mean \pm SEM) for sows stall-housed throughout the gestation (Control, $n = 53$), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, $n = 56$) and sows housed in groups from insemination to farrowing (Group, $n = 58$), belonging to young (parity 0-1; $n = 49$), mid (parity 2-4, $n = 95$), and old (parity 5-7, $n = 24$) parity groups. The non-transformed (raw) mean and SEM values are presented. Brackets connect treatments with significant differences, * $P < 0.05$; T: Tendency, $P = 0.067$.

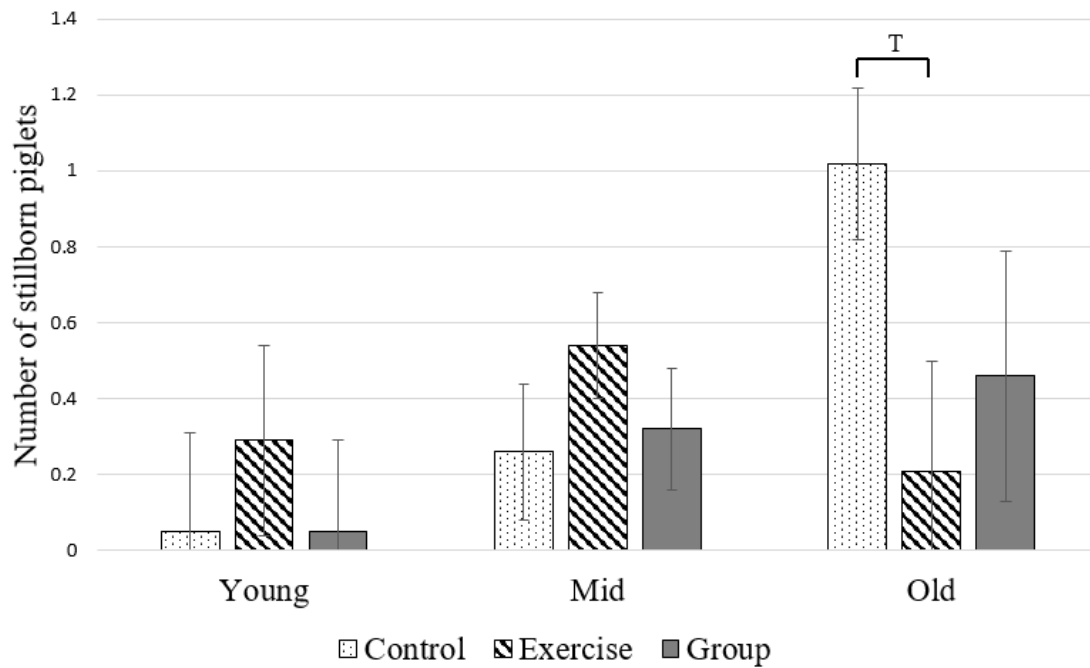


Fig. 6.4. Number of stillborn piglets (mean \pm SEM) for sows stall-housed throughout the gestation (Control, $n = 53$), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, $n = 56$) and sows housed in groups from insemination to farrowing (Group, $n = 58$), belonging to young (parity 0-1; $n = 49$), mid (parity 2-4, $n = 95$), and old (parity 5-7, $n = 24$) parity groups. The non-transformed (raw) mean and SEM values are presented. Brackets connect treatments with differences, T: Tendency, $P = 0.069$.

Table 6.1. Piglet ponderal index (PI), body mass index (BMI) and liveborn piglet mortality proportion for sows stall-housed throughout the gestation (Control, n = 53), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, n = 56) and sows housed in groups from insemination to farrowing (Group, n = 58). The non-transformed (raw) mean and SEM values are presented.

Variable	Control		Exercise		Group		F-value	P-value
	Mean	SEM	Mean	SEM	Mean	SEM		
Ponderal index ^a	65.83	1.42	64.81	1.47	66.65	1.51	0.51	0.599
Body mass index ^b	18.08	0.34	18.07	0.35	18.56	0.36	0.78	0.461
Liveborn piglet mortality proportion	0.11	0.02	0.14	0.02	0.12	0.02	0.84	0.433

^a birth weight/(crown-rump length)³;

^b birth weight/(crown-rump length)².

6.3.2 Placental parameters

Placental development variables did not differ between treatments (Table 6.2).

Old parity sows tended to have heavier placentas than young and mid parity sows, which did not differ (Young: 220.12 ± 17.72 , Mid: 230.37 ± 13.72 , Old: 276.12 ± 19.42 ; mean \pm SEM, g; $F_{2,26.5} = 3.26$, $P = 0.054$). Old parity sows also tended to have lower placental efficiency than young and mid sows, which did not differ (Young: 6.21 ± 0.42 , Mid: 6.23 ± 0.30 , Old: 5.20 ± 0.47 ; mean \pm SEM; $F_{2,28.1} = 2.60$, $P = 0.092$). However, the effects of parity group need to be interpreted with caution, as the old parity group was represented by the low number of sows (n = 6). There was no effect of parity group on other placental parameters (data not presented).

Table 6.2. Placenta variables (mean \pm SEM) from sows stall-housed throughout the gestation (Control, n = 12), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, n = 12) and sows housed in groups from insemination to farrowing (Group, n = 12). The non-transformed (raw) mean and SEM values are presented.

Variable	Control		Exercise		Group		F-value	P-value
	Mean	SEM	Mean	SEM	Mean	SEM		
Surface area (cm ²)	879.01	35.45	870.38	40.15	857.64	39.03	0.07	0.932
Areolae density ^a (cm ²)	1.27	0.08	1.26	0.09	1.21	0.08	0.17	0.846
Total areolae	1221.33	82.84	1195.36	93.65	1078.16	91.06	0.69	0.512
Placental weight (g)	226.19	14.56	247.72	15.53	252.70	15.28	1.54	0.236
Placenta efficiency ^b	6.21	0.33	5.78	0.36	5.65	0.35	1.21	0.315
Placental vascularization	3.26	0.53	3.39	0.61	3.18	0.57	0.04	0.965

^a total areolae/surface area;

^b piglet birth weight/placental weight.

6.3.3 Piglet viability

There was a significant interactive effect of sow treatment and parity group on piglet latency to reach the teat ($F_{4,71} = 3.62$, $P = 0.010$). Piglets from mid E sows tended to have greater latency to reach the teat than piglets from mid C sows, with piglets from mid G sows being intermediate; but within the old parity group piglets from C sows had a significantly greater latency to reach the teat than piglets from E and G sows, which did not differ (Fig. 6.5). Piglets from old C sows had significantly greater latency to reach the teat than piglets from young ($P = 0.033$), and mid C sows ($P = 0.003$). Piglets from young E sows tended ($P = 0.097$) to have greater latency to reach the teat than piglets from old E sows, with mid E sows being intermediate. Piglets from G sows did not differ in their latency to reach the teat across different parity groups. However, this interactive effect needs to be interpreted with caution, as the old parity group was represented by the low number of sows across all treatments (Old C: n = 3; Old E: n = 5; Old G: n = 4). There was also a tendency in piglets from G sows to have lower latency to reach the teat in comparison to piglets from C and E sows, which did not differ (C: 1.43 ± 0.03 , E: 1.51 ± 0.03 , G: 1.38 ± 0.04 ; mean \pm SEM; $F_{2,71} = 2.83$, $P = 0.066$).

There was no effect of treatment (Table 6.3), parity group, or interactive effect of treatment and parity group on farrowing duration, farrowing duration per piglet and piglet latency to stand.

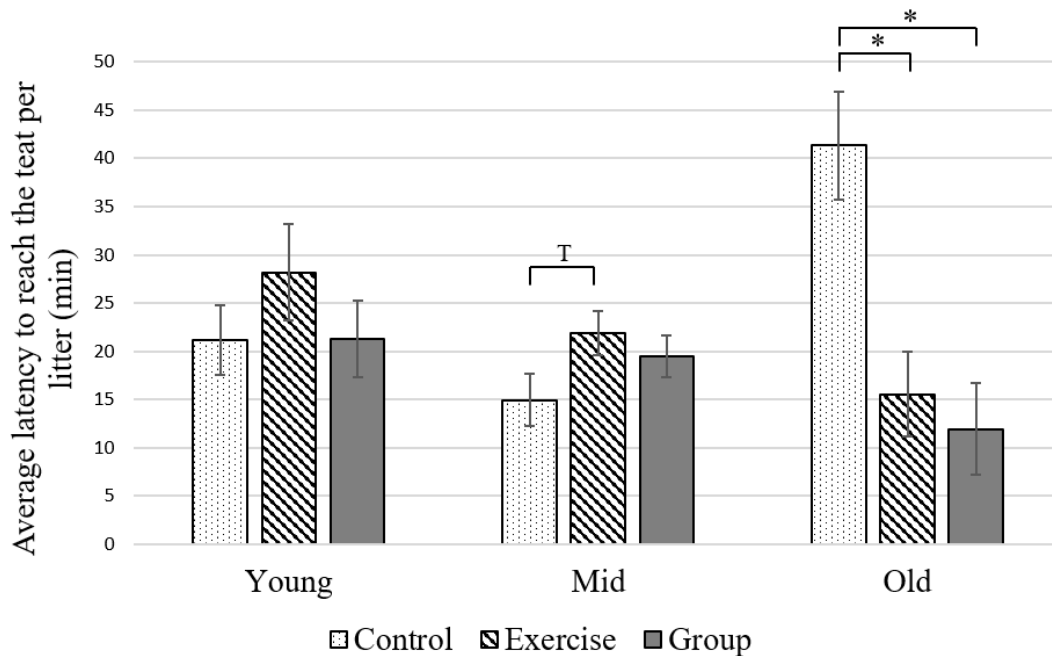


Fig. 6.5. Average latency to reach the teat per litter (min) for piglets from sows stall-housed throughout the gestation (Control, $n = 24$), stall-housed sows walked for 160 m once per week (Exercise, $n = 27$) and sows housed in groups from insemination to farrowing (Group, $n = 36$), belonging to young (parity 0-1; $n = 20$), mid (parity 2-4, $n = 55$), and old (parity 5-7, $n = 12$) parity groups. The non-transformed (raw) mean and SEM values are presented. Brackets connect treatments with differences, T: Tendency, $P = 0.061$.

Table 6.3. Total farrowing time and farrowing duration per piglet, for sows stall-housed throughout the gestation (Control, n = 24), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, n = 27) and sows housed in groups from insemination to farrowing (Group, n = 36), and their piglets' latency to stand (mean \pm SEM). The non-transformed (raw) mean and SEM values are presented.

Variable (mins)	Control		Exercise		Group		F-value	P-value
	Mean	SEM	Mean	SEM	Mean	SEM		
Farrowing duration	255.88	36.68	315.60	35.33	245.11	33.22	0.67	0.514
Farrowing duration per piglet	24.49	6.80	26.32	6.60	20.12	6.22	0.46	0.636
Latency to stand	11.41	1.49	11.13	1.48	11.18	1.39	0.40	0.670

6.4 Discussion

In the current study, the effects of providing periodic exercise to pregnant stall-housed sows on sow reproductive performance, placental characteristics and piglet viability measures were investigated. Providing stall-housed sows with access to a low level of exercise once per week throughout gestation benefited the reproductive performance of older parity sows, increasing liveborn and tending to reduce stillborns, and also affected the total litter size. Sows in groups showed similar benefits, which suggests that freedom of movement plays a role in sow reproductive performance. This result has been found repeatedly in previous literature: Lammers et al. (2007) found that sows housed in deep-bedded group hoop barns had a higher number of liveborn piglets and tended to have greater total litter size in comparison to the sows housed in stalls during gestation. Similarly, Tan (2015) reported that group-housed sows had more liveborn piglets than stall-housed sows, and they also had a tendency for higher total litter size. Seguin et al. (2006) found that group-housed gestating sows had higher total litter size than stall-housed sows. In terms of the number of stillborn piglets, Chapinal et al. (2010) and Weng et al. (2009) found that group-housed sows in pens with electronic sow feeder (ESF) and in groups with individual feeding had fewer stillborns than stall-housed sows. Lammers et al. (2007) also found that sows housed in hoop barns tended to have fewer stillborn piglets in comparison to sows housed in gestation stalls. Similarly, Brown (2015) reported that sows which were mixed into groups at weaning had significantly fewer stillborn piglets in comparison to sows which were

stall-housed for the first five weeks of gestation and then mixed. Schenck et al. (2008) showed that stall-housed gilts receiving periodic exercise at the levels higher than those used in the current study did not demonstrate any difference in the total litter size and numbers of liveborn and stillborn piglets in comparison to gilts, stall-housed throughout gestation, which is in agreement with the results of the current study for the young parity group. The increase in the number of liveborn piglets and decrease in the number of stillborn piglets in sows having access to a greater freedom of movement could be related to higher muscular weight (Marchant and Broom, 1996) and improved cardiovascular fitness (Marchant et al., 1997) in these animals. These parameters were previously demonstrated to reduce the farrowing duration and piglet birth interval (Fraser et al., 1997), which could decrease the incidence of neonatal asphyxia and result in higher piglet survivability (Lammers et al., 2007). However, in the current study sows from different treatments did not differ in the duration of parturition and farrowing duration per piglet, hence the physiological mechanisms that could result in changes to reproductive performance were not revealed. Alternatively, it could be assumed that sows receiving exercise (both G and E sows) were more stressed than stall-housed throughout gestation sows due to aversive interactions with conspecifics or higher incidence of interaction with handlers. Kranendonk et al. (2006) have previously shown that prenatal stress induced by hydrocortisone-acetate administration improved piglet survival and results in a higher number of liveborn piglets in comparison to non-stressed sows, possibly through promoting fetal organ maturation by stress hormones. However, Kranendonk et al. (2006) also reported higher liveborn piglet mortality in prenatally stressed piglets, indicating that prenatal stress improved short-term, but not long-term survival, which was not observed in the current study. As the main differences in sow reproductive performance in the current study were observed in the old parity group, which included the lowest number of animals in comparison to young and mid parity groups, further research with the use of a larger sample of older parity sows is needed to understand the physiological relationship between providing a greater freedom of movement and sow reproductive performance.

Piglet birth weight did not differ across treatments, which is consistent with previously reported findings for sow housing systems with different levels of access to a greater freedom of movement. For example, Broom et al. (1995) reported no difference in the piglet birth weight between stall-housed sows and sows housed in small groups with feeding stalls or in large

groups with ESF. Similarly, Salak-Johnson et al. (2007) did not find any differences in piglet birth weight across sows housed in stalls or groups with different space allowance. The same effects were reported by Schenck et al. (2008) and Harris et al. (2013) for periodically exercised and stall-housed gilts. Taking into account that housing sows in groups for gestation, and thus providing access to freedom of movement was previously demonstrated to increase litter size (Seguin et al., 2006), which is possibly related not only to exercise per se but also to reduced stress levels due to having a greater freedom of movement, the lack of increase in piglet birth weight could be explained by limited uterine capacity and a higher proportion of piglets with lower birth weight as a result of intrauterine crowding (Ji et al., 2017). However, in the current study there was no difference in litter size between treatments within the young parity group, suggesting that providing greater freedom of movement was not a strong enough factor to produce measurable benefits for reproductive performance in young sows.

Although the presence of intrauterine crowding leading to intrauterine growth restriction (IUGR) is expected in multiparous species, there was no IUGR effect observed in the current study, based on the values of piglet ponderal and body mass indices. Low ponderal and body mass indices are considered to be indicators of severe IUGR and lower piglet survivability (Amdi et al., 2013). However, in the current study these indices did not differ across treatments, and the obtained values of body mass index were higher than those defined as indicative of mild IUGR in the study of Amdi et al. (2013). Based on this information, it can be concluded that the observed increase in litter size in older sows due to providing a greater freedom of movement at the levels used in this study did not cause IUGR.

The lack of impact of the level of access to a greater freedom of movement on liveborn piglet mortality is in agreement with the results of Harris et al. (2006), who did not find any difference in liveborn piglet mortality between gilts stall-housed throughout gestation and gilts housed in small groups. In contrast, Anil et al. (2005) reported a significantly lower liveborn piglet mortality rate in sows housed in group pens with ESF in comparison to stall-housed sows. Karlen et al. (2007) also reported a higher number of weaned piglets in litters from group-housed on deep litter sows in comparison to sows housed in conventional stalls. Similarly, Schenck et al. (2008) reported higher liveborn piglet mortality in stall-housed gilts in comparison to gilts, receiving exercise five days per week at low (610 m per week) and high (1525 m per week) levels. The above-mentioned findings could be associated with the decreased time taken to lie

down by exercised sows, which could reduce the chance of piglets moving under the sow after the onset of the descent of her body to the ground. This effect could be observed due to improved sow mobility resulting in more controlled posture changes linked to increased overall fitness and hence more muscle control as the result of exercise (Harris et al., 2013). The levels of exercise used in the current study were much lower in terms of both frequency and duration than in the study of Schenck et al. (2008) and than the levels of exercise accessible to group-housed sows, which has been shown to be greater than when sows were encouraged to exercise in the maximum exercise treatment in the same study of Schenck et al. (2008), which might be a reason of the lack of observed differences between treatments.

Parity group tended to affect liveborn piglet mortality in the current study, with older sows tending to have a higher piglet mortality proportion in comparison to young and mid parity group sows, which did not differ. In contrast, Smith (2011) previously demonstrated that gilts have higher liveborn piglet mortality in comparison to multiparous sows. This discrepancy might be due to the fact that in the current study higher liveborn piglet mortality in gilts could be evened out by lower liveborn piglet mortality in the first parity sows, as both gilts and parity 1 sows were assigned to the same parity group, or due to the low number of sows representing the old parity group in the current study. This was not an effect of providing a greater freedom of movement, as there was no interactive effect of sow treatment and parity group on liveborn piglet mortality in the current study. At the same time, Smith (2011) also reported lower piglet birth weights in gilts in comparison to multiparous sows, and Chapinal et al. (2010) reported lower piglet birth weights in gilts than in sows of parity 2-4, which is in agreement with the results for young and mid parity groups in the current study. This finding could be explained by different nutrient partitioning in pregnant gilts, which use more of the available nutrients for their own body growth to achieve physical maturation, than for piglet growth (Matheson et al., 2018).

Previous human medical research suggests that exercise has positive effects on fetoplacental growth resulting in faster placental development that improves the placental function (Clapp et al., 2000). One of the main functions of the placenta is delivering nutrients to the developing fetus, and this function is largely determined by the size of the placenta (its weight and surface area), placental efficiency and level of placental blood supply (van Rens et al., 2005). Additionally, areolae density and the total number of areolae were demonstrated to be important indicators of piglet prenatal and postnatal survival (Baxter et al., 2008). In the current study, no

differences in placental traits between treatments were observed. Similarly, Harris et al. (2013) reported no effect of providing gilts with periodic exercise for 30 mins three times a week on placental weight in comparison to stall-housed gilts. However, in the latter study the peak of pulsatility index, as measured by ultrasound, in exercised gilts was reached earlier than in control gilts. The authors hypothesized that an early decline in vascular resistance is related to earlier dilation of uterine and placental blood vessels, which would increase blood flow to the developing fetus. However, in the current study no difference in placental vascularization across treatments was observed. This might be due to a few reasons: first, the levels of exercise applied in the current study could be too low to impact the level of placental blood supply. Second, placental data were collected across all parities of sows, and not concentrated to old parity sows. As a result, only six sows from the studied sample belonged to the old parity group, whilst young parity group was represented by 10 sows, and mid parity group was represented by 20 sows. A larger sample size, as well as focusing on old parity sow data might be needed to demonstrate the mechanisms by which providing a greater freedom of movement can impact placental development, as well as reveal the link between improved reproductive performance in old parity sows and their placental traits.

One of the positive effects of providing a greater freedom of movement observed in the current study was improved piglet viability, as determined by the reduced latency to reach the teat in piglets born from G and E sows from the old parity group. However, only less than 1/3 of the total number of sows used for the current study belonged to the old parity group. Latency to reach the teat and latency to first suckle were previously determined as critical postnatal survival factors (Baxter et al., 2008). Timely colostrum intake is crucial for early postnatal survival, as piglets do not have brown adipose tissue which in other species is used for thermogenesis (Hou et al., 2018) and also newborn piglets have very low overall body fat content (around 1.7%, according to Seerley and Poole (1974)). Thus, colostrum is the main source of providing energy to maintain homeothermy in neonatal piglets (Quesnel et al., 2015). Additionally, due to the fact that piglets are born without immune protection, through suckling colostrum they acquire not only nutrients but also maternal immunoglobulins, which provide passive immunity (Rooke and Bland, 2002). The influence of sow treatment on piglet latency to reach the teat in the current study may be due to changes from both neonatal and maternal sides. It can be hypothesized that higher levels of sow locomotor activity during gestation resulted in giving birth to piglets with

higher vigour. Piglets from non-exercised sows could be more lethargic due to hypoxia which they faced as a result of prolonged piglet birth intervals (Edwards and Baxter, 2015); however, this relationship was not confirmed by the farrowing duration results in the current study. Heavier piglets were previously reported to have higher vigour and be more successful in winning teat disputes with other littermates (De Passille and Rushen, 1989), but in the current study the piglet birth weight did not differ across treatments and piglet birth order was not recorded. Another possible reason could be reduced restlessness in sows during farrowing, which allowed piglets to access the sow's udder more easily (Edwards and Baxter, 2015). The levels of maternal restless behaviour during farrowing were not measured in the current study, but previous research suggests that group-housed sows show more restlessness during farrowing and in early lactation than stall-housed sows, possibly due to increased levels of frustration related to unexpected restriction in access to a greater freedom of movement in the farrowing crate, or maybe simply because group-housed sows are fitter and it is easier for them to change postures (Boyle et al., 2002). These effects were not observed in the current study, as piglets from the sows which had access to certain levels of freedom of movement had reduced latency to reach the teat, hence these sows were supposed to be less restless. As these beneficial results of exercise were observed primarily in the old parity group sows, they could also be related to a small sample size which represented this group, and larger sample size could be needed to study the relationship between maternal access to exercise and piglet latency to reach a teat in more detail.

Other measures of piglet viability, such as farrowing duration, farrowing duration per piglet and piglet latency to stand were not influenced by sow treatment in the current study. Even though farrowing kinetics and piglet vigour are widely recognized to be indicators of piglet survival (Edwards and Baxter, 2015), there is a lack of studies comparing these parameters in sows across different housing systems with different levels of access to a greater freedom of movement. In one of the previous studies relevant to this topic, Harris et al. (2013) reported no differences in piglet birth interval and the length of parturition across stall-housed throughout gestation and exercised gilts. Based on these results and also on the data recorded in the current study it can be concluded that providing periodic exercising at the levels used in the current study and the study of Harris et al. (2013), or voluntary access to a greater freedom of movement in group housing system do not affect farrowing kinetics, as measured by farrowing duration and

farrowing duration per piglet. This is possibly because the levels of exercise received by periodically exercised and group-housed sows in these studies were not sufficient to measurably improve farrowing kinetics through enhancing uterine and overall muscular fitness.

In general, the mechanisms by which providing a greater freedom of movement can impact sow reproductive performance were not revealed in this study. For example, a shorter farrowing duration, farrowing duration per piglet, as well as placental areolae count and areolae density could explain the parity specific reproductive effects, but no impact of these parameters on sow reproductive performance was observed. Similar to the placental measures, farrowing duration and farrowing duration per piglet data were collected from sows across all parity groups, without focusing on old parity sows. Again, using a larger sample consisting of old parity sows could potentially reveal the mechanisms by which providing a greater freedom of movement can influence sow reproductive performance and piglet viability. However, the relationship between sow parity number and improved reproductive performance as a result of having access to a greater freedom of movement needs to be first confirmed by analyzing the data from sample of sows balanced by parity, as currently it is unknown why providing exercise influenced reproductive performance in older sows only.

6.5 Conclusions

Our findings suggest that providing stall-housed gestating sows with exercise by walking for 160 m once a week did not bring any measurable benefits in terms of placental development and farrowing kinetics in comparison to sows housed in group settings and stalls. Periodic exercise positively affected reproductive performance and piglet vigour in older parity sows, but the physiological mechanisms of these effects were not revealed in the current study. Further investigation, including the use of larger sample size, is needed to determine the causes of the observed effects.

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7. GENERAL DISCUSSION AND CONCLUSIONS

The studies forming this thesis investigated whether gestating sows and gilts were motivated to access a greater freedom of movement, if the motivation of a sow to leave her stall was influenced by sow satiety and, how providing low-level periodic exercise impacted sow behaviour, stress physiology, reproductive performance, placental development, as well as piglet viability and the behavioural response of piglets to stress tests. The purpose of these objectives was to understand whether providing stall-housed gestating sows with periodic exercise at a low level (160 m, once per week) would be a viable option for enhancing stall-housed sow well-being. Additionally, the mechanisms through which periodic exercise could impact sow physiology and reproductive performance were investigated, and this information would add to the body of evidence on sow health and functioning. The results of this research were provided to the Pig Code Technical Committee for their five year review of the Canadian Code of Practice for the Care and Handling of Pigs to help inform decisions on the housing requirements of gestating sows in Canada post 2024. The results of these studies also have a wider application to pig farming worldwide. Keeping sows in stalls remains a popular housing option, with the majority of sows in commercial swine operations kept in the close confinement of stalls for at least a proportion of their production cycle (i.e. breeding stalls) if not for the entirety (gestation stalls and farrowing crates). Therefore, the options to remove confinement and alternatives to confinement are being extensively explored for both gestating and farrowing sows. The strong societal concern regarding sow confinement, paired with the body of scientific evidence on the mismatch between the sow's biological needs and building design in restrictive housing systems, led multiple countries to making progress towards providing alternatives to housing sows in close confinement (Baxter et al., 2018).

The research within this thesis has been able to identify the presence of motivation for a greater freedom of movement in stall-housed female pigs. Chapter 3 found that gilts were equally motivated to access additional feed and movement, and sows had a greater level of

motivation to access additional feed than to access movement. The difference in gilt and sow motivation for feed could be explained by sows being feed-restricted while recovering from the previous lactation and hence feeling more hungry than gilts. However, gilts and sows did not differ in their proportions of time spent in exploratory behaviour when out of the stall, which highlighted the importance of exploration for both gilt and sow behavioural repertoires (Stolba and Wood-Gush, 1984). Read et al. (2020) demonstrated that sows receiving 2.5 kg of a standard gestation ration were by 15% more active (they stood and walked more) than the sows fed with commercial dry sow feed ad libitum: based on this information, the equal levels of locomotion when being outside of the stall in gilts and sows in our study could suggest the presence of similar levels of hunger in female pigs with different prior stall experience, or a similar need for movement in both groups, which may be linked to opportunities to explore and seek more feed. Chapter 4 identified that the level of motivation to exit the stall was reduced when high fibre feed was provided to sows in the stall, supporting the idea that providing high fibre feed reduces sow activity levels through increasing satiety (Zonderland et al., 2004), and additionally that there was a strong exploratory/foraging component in sows' motivation to leave the stall. This was expected, given that for feed-restricted sows food is a resource of high value (Patterson-Kane et al., 2008) and that sows in intensive systems remain hungry and are motivated to continue foraging after they have finished their meal of concentrated food (D'Eath et al., 2018). In the current study, the observed reduction in sow motivation to leave the stall was assumed to be linked to greater satiation and hence possibly a lower motivation to forage. Previous studies (Lawrence et al., 1989; Robert et al., 1997) investigating hunger and feeding motivation in pigs using operant responding tasks have consistently found reductions in the operant response when feeding regimes achieved satiation, either through diet type or feed quantity, which is in agreement with the findings of the present work. However, in our study, despite a lower level of operant responding, sows continued to exit the stall when fed ad-libitum, demonstrating their intrinsic need in continuing exploration. Because no measures were taken (such as blood hormone levels) to confirm, it cannot be truly known whether the sows on the ad-libitum treatment were satiated. However, it is considered unlikely that sows from the ad-lib treatment remained hungry due to the methodological approach that was used and that behaviourally, the sows had ceased eating prior to testing starting.

When outside of the stall, both gilts and sows in the first study (Chapter 3) and sows at different levels of satiety in the second study (Chapter 4) spent the highest proportion of time in exploratory behaviour and lower and equal proportions of time in locomotion and snout to snout contact respectively. These results were expected if thinking about sow behavioural needs, including the intrinsic need to move and to interact with conspecifics (Stolba and Wood-Gush, 1984). An animal having control over its environment is considered one of the most important prerequisites for having good welfare (Broom, 1991); a loss of control leading to the development of chronic stress (Wiepkema, 1987), which has detrimental consequences for sow health and mental well-being (Barnett et al., 2001; Spooler et al., 2009). The importance of having control over their environment and having a greater freedom of movement as a part of this control is further supported by the fact that animals were presented with the operant panel daily and chose to leave the stall every day when given an opportunity. Therefore, the results of the first and second studies highlight the importance of the need for sow housing system to meet the behavioural needs of sows, with providing sows a greater freedom of movement being a priority.

The novelty of this research lay in exploring the welfare aspects of sow confinement in a stall; to date there has been little research asking questions on the value of freedom of movement to stall-housed sows. Using an operant conditioning technique to measure the motivation of stall-housed gestating sows to access a greater freedom of movement was also a novel approach; it specifically helped to understand the sow's response to this, which has not been considered previously. Rather, previous research has focused on the balance of welfare measures in sows in stalls vs sows in groups (Hulbert and McGlone, 2006), or what factors influenced sows' use of free-space (Rioja-Lang et al., 2013). Additionally, our study used an improved version of an operant panel that contained two buttons, so we could make sure that the sow was making a defined choice when selecting an active button to work for access to the reward, rather than the presses made by chance or for exploration. Due to this panel design, we were able to measure the precision with which the sows made their choice as further evidence.

Previous operant conditioning studies conducted in gestating sows have explored sow motivation to access different types of enrichment (Jensen and Pedersen, 2007; Elmore et al., 2011; Elmore et al., 2012), and one explored the motivation of sows to access a greater freedom of movement in a barren pen (Haskell et al. 1997). The work of Haskell et al. (1997) found that

sows are willing to work for access to 41.5 m² of additional space, but this motivation was measured only during four days before parturition, and the effects of confinement in a small home pen (2 × 2 m), not a conventional gestation stall, were studied. As for the effects of high fibre supplementation, previous studies (Lawrence et al., 1988; Lawrence et al., 1989; Robert et al., 1997; Ramonet et al., 2000; Jensen et al., 2012) mostly looked at the motivation of pigs for a food reward when their levels of satiety were altered by feeding high fibre. To the best of our knowledge, no earlier work has explored the motivation of pigs for resources other than food when kept at different levels of satiety using operant tests, and this was the novelty of our work. The only comparative work is that of Hemsworth et al. (2011) who used choice tests to evaluate the effects of feed restriction on the choice behaviour of 15-20 weeks old pigs when offered access to social contact vs bedding in a Y maze (Hemsworth et al., 2011). Assessing operant responding and choice behaviour under different levels of satiety can provide valuable information about whether changing the satiety level can alter an animal's motivation for different non-consumable resources, and ultimately whether these resources can be compensated for additional feed. However, difficulty in determining the level of satiety precisely creates a limitation for the use of this approach. In the current study, the amounts of feed received by the sows were based only on their previous feed consumption levels, which is in line with the previous research (Lawrence et al., 1989; Robert et al., 1997; Hemsworth et al., 2011). The additional measures of satiety, such as levels of blood hormones (leptin and ghrelin (Bakheet et al., 2020)), were not taken in the current study, as well as in the previous swine experiments conducted in this field, but their use can potentially be beneficial for future research to confirm how the behavioural response relates to the physiology.

An additional strength of our work lay in using the sow as her own control (Chapter 3). It was possible to train and test each animal for both exercise and food rewards, as demonstrated by the high level of precision of the AB pressing, maintained when the AB and DB were swapped over. This approach was helpful for assessing the motivation of the individual for time out of the stall against a comparative reward of known high value, helping to understand the relative strength of their motivation for each reward. In contrast, previous studies (Hemsworth et al., 2011; Elmore et al., 2012) used groups of different animals when testing their motivation for different resources, and as such their results could be affected by individual differences.

Despite that the motivation to access time out of the stall was present, in Chapter 5 this research identified that providing stall-housed female pigs with periodic exercise through walking for 160 m once per week throughout gestation did not improve sow comfort, as indicated by lower levels of lying and increased sitting in stall-housed sows. Additionally, exercise did not reduce the stress coping response, as indicated by an increased performance of stereotypies in stall-housed sows. Previous work has found that gilts exercised for 30 mins, three times per week from mid to late gestation had reduced restlessness and possibly improved comfort, as determined by gilts performing fewer postural changes and sitting less in comparison to gilts receiving no exercise (Harris et al., 2013). That stall-housed exercised gilts sat less in the work of Harris et al. (2013) may be due to the fact that gilts received a greater amount of exercise than in the present study. However, the level of exercise used by Harris et al. (2013) is not practically achievable in commercial barn settings and this is why the present research needed to be conducted. In both our study and the study of Harris et al. (2013) measurements of the duration of time spent in postures were taken. However, Harris et al. (2013) recorded gilt postures for a much longer period of time (over a 24 hour period and with continuous observation of duration and frequency of posture changes). Additionally, the frequency of postural changes was not recorded in the present work, which could also explain why the results differ from those found by Harris et al. (2013). At the same time, group-housed sows in our study performed fewer stereotypies in early and mid gestation and showed higher levels of comfort, as indicated by a lower frequency of sitting and higher frequency of lying in group-housed sows in comparison to stall-housed sows with or without access to periodic exercise. This suggested that group-housing, but not periodic exercise improved sow welfare in the current study. These results could be explained by the group settings giving sows more control over their environment and providing a greater freedom to move and an opportunity to change postures without the spatial constraints of a stall, which could not be achieved by periodic exercise.

To improve the assessment of the gestation environment, a further novelty of the present research lay in our attempt to evaluate the impact of the gestation environment on sow welfare via measures of chronic and prenatal stress. In particular, results of the piglet behavioural stress tests indicated a change in piglet stress response linked to the gestation environment and the level of freedom of movement experienced by the gestating sow in different gestation management systems. These findings were particularly important as this work was one of the

first works exploring prenatal stress caused by confinement during gestation. Previous work has often tried to recreate a stress in a controlled manner, such as by oral administration of hydrocortisone-acetate (Kranendonk et al., 2005; Kranendonk et al., 2006; De Groot et al., 2007; Mack et al., 2014) or ACTH injections (Otten et al., 2004; Otten et al., 2007; Kanitz et al., 2006). In contrast, our study tested the real-world stressors experienced by gestating pigs in different management systems. The results of this study emphasized the importance of using different approaches to understand the effects of stress. They also highlighted the need for wider use of chronic measures for the assessment of stress experienced by gestating sows in different housing systems.

Providing periodic exercise benefitted sow reproductive performance and piglet viability, but only in the old parity group, and these results were comparable to the results of group-housed sows (Chapter 6). However, the mechanisms by which periodic exercise impacted sow reproductive function and piglet quality were not revealed in this study, as placental characteristics and farrowing kinetics did not differ across treatments. Modelling of the economic assessment showed that an increase in sow performance in a proportion of the herd concentrated to the older parity sows could reduce the production costs in Canada by \$0.94/hog arising from spreading the cost of production over an increase in pig meat produced per sow. However, the additional labour required to exercise sows would also increase the cost of production by \$2.94 per hog (Tokareva et al., 2020). Overall, providing periodic exercise increases the cost of production by \$2.00/hog. Whether this is cost effective will depend on the market price of pig meat. However, if exercise was provided only to parity 5+ sows, assuming that they represent 26.5% of the herd, it would increase the cost of production only by \$0.78 per hog. Given the reduction in the production costs from the increase in performance in the older parity sows, providing exercise to parity 5+ sows only would actually decrease the overall cost of production by \$0.16. But further studies using larger and balanced by parity group sample size are needed in order to confirm the benefits of providing periodic exercise to parity 5+ sows only.

The novelty of the third and fourth experiments (Chapters 5 and 6) lay in exploring the effects of providing infrequent low-intensity periodic exercise on multiple aspects of gestating sow welfare. The question on the benefits of providing periodic exercise has not often been asked, because moving to a group-housing system was considered to be better. The few papers on the effects of periodic exercise on the welfare of gestating sows studied levels of exercise

which would unlikely be practical to implement in commercial conditions due to high labour requirement. This work includes: forcing sows to walk 2 km daily from day 35 to 108 of gestation (Ferkett and Hacker, 1985), encouraging sows to walk/run for 122 mins or 427 mins per day, five days/week between day 35 and 110 of gestation (Schenck et al., 2008), or exercising sows for 30 mins, three days/week from day 40 to 104 of gestation (Harris et al., 2013; Kaminski et al., 2014). Such levels of exercise made these studies more theoretical than applied. Simply focusing on providing exercise would ignore all the other welfare benefits that group-housing can provide to sows. Therefore, the current research made an attempt to evaluate numerous aspects of sow welfare, including physical, physiological and behavioural measures. This was done to try and discover the mechanisms by which exercise may influence different parameters of sow physiology and her welfare. One of the methods used for this purpose was the analysis of hair cortisol, which is a non-invasive and novel (for pigs) technique for measuring the levels of cortisol over longer periods of time, providing a means to evaluate chronic stress levels (Casal et al., 2017). Whilst our research did not find any effects of the sow gestational environment on this measure, we believe that this approach will be useful for measuring chronic stress in the future. This idea is supported by the results of a recent study, which found a difference in hair cortisol levels between stall-housed and group-housed parity 0-1 gestating sows, with stall-housed sows having higher hair cortisol concentration (Everding et al., 2020). A higher level of cortisol is assumed to be an indicator of higher levels of stress (Bacci et al., 2014; Trevisan et al., 2017). In the study of Everding et al. (2020) hair samples were collected at day 37 and 111 of gestation, with hair cortisol concentration tending to be lower at day 37. These results suggest that further studies may benefit from not using the hair growth from the last trimester of pregnancy. Using the hair regrowth from the whole gestation cycle in our study could lead to the hair cortisol levels being evened out between treatments due to the rapid rise of cortisol levels during the third trimester of pregnancy as a physiological response of an organism to impending labour (Dorr et al., 1989). In the current study, we aimed to analyze the hair from the whole growth period to explore if this is a valid approach to understanding gestational stress. Taking one sample representative of the whole period of study could save labour and laboratory analysis costs in comparison to shaving and analyzing hair from multiple periods over the course of gestation. Additionally, future studies would benefit from the use of larger sample size, as it could decrease the likelihood of a Type II error (Columb and Atkinson, 2016). Also, the cause of

high individual variation in hair cortisol levels in our experiment (which was also reported in previous studies) remains unclear, therefore further studies need to be conducted in order to confirm that hair cortisol is an accurate measure of gestational stress in sows and that the interpretation of this measure is correct. The development of and more extensive use of methods to evaluate chronic stress is the approach needed (Heimbürge et al., 2019), for the evaluation of housing system effects on sow welfare, which links to answering a more general question – the question of quality of life in farmed pigs.

The limitations of this research included relatively small sample sizes used for the operant conditioning experiments. However, the use of such small samples is typical for the motivation studies, considering that each animal involved needed to be individually trained and tested over the course of multiple consecutive days, which is labour intensive. Additionally, we faced multiple technical challenges with an operant panel. Even being maximally protected from animals, the operant panel still had a relatively fragile construction and needed to stay plugged to the battery via cable during the training and testing: a connection that could easily be destroyed by a curious sow. Moreover, pigs performed their exploratory behaviour quite actively, by pushing novel objects hard, trying to chew or bite them, with these factors having a negative impact on equipment longevity. This challenge in using the panel has implications for the ability to widely use this type of approach to ask animals about their environment.

One of the main limitations of the third and fourth experiments (Chapters 5 and 6) lay in an underrepresentation of sows from the old parity group. This was because the parity groupings in the current study were specifically designed to have biological relevance, and this study was conducted in a herd of sows which represented the commercial herd structure, so the majority of animals were younger than parity five sows. Therefore, it needs to be understood that there is a chance that the significant differences in sow reproductive performance may not hold true with a larger sample size. The outliers were not removed from the data on reproductive performance because they were biologically representative of sow reproductive performance, with some sows having large litters and other sows having small litters, and that alone could have been linked to the treatments, as we were testing for the effect of the treatment on reproductive performance. This may have had an influence on the Type I error rate. However, calculations to control outliers were performed, and additional simple non-parametric tests were used to test assumptions. Nonetheless, having a larger sample size, and an equal sample size of sows over

parity groups could help to reduce the error rate which needs to be considered in the future. Additionally, the limitation of a small sample size extends to the placental characteristics, hair cortisol concentration and piglet viability measures (farrowing duration, farrowing duration per piglet and piglet latency to stand), as no difference observed in these parameters could be due to the fact that used subsamples of sows were non-balanced by parity group, which was related to the structure of the studied herd. For the piglet viability measures, a further lack of balance by parity group was caused by multiple camera failures. A small sample size could increase the likelihood of a Type II error, which would decrease the statistical power of the study (Shreffler and Huecker, 2020). Further research, including larger sample size and equal parity distribution, is needed to verify the connection between providing periodic exercise and improved sow reproductive performance, and also to reveal the physiological processes by which this connection is established.

The results of the piglet behavioural response to stress tests (Chapter 5) could be open to more than one interpretation. The present study found that piglets from periodically exercised and group-housed sows moved less in the novel object test than piglets from stall-housed throughout gestation. Previously, this has been interpreted as an indicator of increased fearfulness in piglets subjected to the same test (Kranendonk et al., 2007). However, based on our observations we interpreted that in our study higher activity in the novel object test indicated higher levels of anxiety, as the piglets were observed to display chaotic patterns of quick movement, presumably when piglets were trying to escape the novel object/test arena. This hypothesis was in agreement with the vocalization results of the isolation test, where piglets from exercised sows vocalized less than piglets from other treatments, and hence they were presumably less stressed. Looking at the piglet locomotor activity in stress tests from this perspective resulted in a different interpretation of the test results in comparison to the study of Kranendonk et al. (2007), and it needs to be validated in future studies. Results of these individual behavioural tests conducted in neonates have previously been based on a rat model (Weaver et al., 2000). Species-specific considerations need to be given to ensure that the interpretation is accurate, as the lack of these considerations could cause evidence misinterpretation in the existing literature. Our research helped to contribute more information for this effort. Our study has shown that behavioural measures need to be incorporated along with physiological measures, as both these measurements can help detect the presence of

prenatal stress. Additionally, it would be beneficial to incorporate prenatal stress measures into sow housing system research in order to understand the effects of gestation systems on offspring. Prenatal stress effects have not been considered sufficiently in previous research when comparing different sow housing systems, and the present work was one of the first to address this issue. Considering prenatal stress when evaluating gestation housing systems would advance our knowledge of the impact of gestation management on animal production in general, as this approach takes into account not only the changes that happen to the pregnant female during gestation but also how these changes influence offspring during prenatal and postnatal periods.

The evidence collected in these studies suggested that providing a greater freedom of movement was valued by gestating sows, and that freedom of movement could reduce levels of stress in these animals and bring some reproductive benefits for older sows. Providing periodic exercise through walking sows for 160 m once a week throughout gestation could bring some benefits to sow welfare, but the level of improvement was not considered sufficient to advise periodically exercising stall-housed gestating sows at the frequency and duration, used in the current work. There are other methods that could be employed to provide sows with higher levels of exercise, such as installing treadmills in the barns, but they would require more research and a new system investment. At the same time, group housing was demonstrated to be a more effective way of providing a greater freedom of movement to stall-housed gestating sows and it also brought more measurable welfare benefits than periodic exercise in our study. Given this and the other advantages of housing in groups, such as fulfilling the sows' intrinsic need to have control over their environment, a transition from stall-housing to the group-housing system is advisable.

This research is highly relevant to the Canadian pork industry, as it provided scientific evidence on which to inform the implementation on the Code recommendation to provide stall-housed gestating female pigs with a greater freedom of movement (NFACC, 2014). However, on a larger scale, this work is applicable to global pig production where the sow is confined for at least some point in her life. Without this work, it could be assumed that providing sows with such an option of having a greater freedom of movement as periodic exercise at the levels achievable in commercial barn settings, would be sufficient to improve sow welfare, and there is no need to take any other actions. However, this would be a very anthropomorphic approach which would consider the situation only from the perspective of the human without taking into

account the needs and perspectives of the animal (Morton et al., 1990). The body of research in this thesis helped to demonstrate that sows are motivated for movement, but they also have behavioural needs for exploration and social contact. Based on the previous research and on the evidence collected in this work, it can be concluded that the needs of the sow can be better met in the group housing settings than by providing periodic exercise by walking sows for 160 m once per week during gestation. Additionally, this work contributed to the further development of methods for evaluating swine welfare, such as operant conditioning testing and measuring of hair cortisol levels. It also evaluated the effects of chronic and prenatal stress in sows receiving periodic exercise in comparison to stall-housed and group-housed sows, which has not been explored previously. Moreover, this research tried to reveal the mechanisms by which having access to exercise can improve sow reproductive performance, which could be used in future studies on sow physiology of pregnancy. To sum up, this work contributed to advancing our understanding of the factors that are important for enhancing the welfare of the gestating sow and the results of this research can be used to improve gestating sow housing systems worldwide.

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APPENDIX A

Table A.1. The latency (s) to push the active button by female swine for different rewards (exercise or feed) and with different prior stall experience (PSE, sow or gilts) and different prior training experience (PTE, exercise reward first or feed reward first; mean \pm SEM). The non-transformed (raw) mean and SEM values are presented.

	Reward		PSE				PTE					
	Exercise	Feed	F-value	P-value	Gilt	Sow	F-value	P-value	Exercise reward first	Feed reward first	F-value	P-value
Latency	9.88 \pm 3.00	8.13 \pm 2.74	0.48	0.490	10.21 \pm 2.80	7.79 \pm 2.93	0.77	0.384	9.54 \pm 2.72	8.46 \pm 3.02	0.10	0.748

Abbreviations: PSE, prior stall experience; PTE, prior training experience.

Table A.2. Percentage of time (mean \pm SEM) spent in locomotion, exploratory behaviour, snout to snout contact and in other behaviours by sows from the high score population (sows that reached a minimum FR of 72; n = 10) with regard to the PSE, BCS, PTE and opportunity number. The non-transformed (raw) mean and SEM values are presented. Where superscripts differ, $P \leq 0.05$.

Behaviour type	PSE				BCS					PTE				Opportunity number				
	Gilt	Sow	F-value	P-value	2	3	4	F-value	P-value	Exercise first	Feed first	F-value	P-value	1	2	3	F-value	P-value
Locomotion	18.49 \pm 1.22 ^a	8.58 \pm 1.49 ^b	38.52	< 0.001	9.02 \pm 2.11	12.62 \pm 1.79	19.37 \pm 1.42	0.13	0.880	14.14 \pm 4.62	16.01 \pm 3.72	0.06	0.829	16.45 \pm 1.14 ^a	13.49 \pm 1.60 ^b	10.66 \pm 1.25 ^b	13.03	< 0.001
Exploratory behaviour	45.19 \pm 9.09	52.17 \pm 9.58	0.15	0.700	63.87 \pm 9.08	48.70 \pm 8.29	39.10 \pm 7.13	1.56	0.225	62.12 \pm 14.50	38.78 \pm 11.76	3.02	0.216	54.21 \pm 6.45	51.82 \pm 9.87	47.81 \pm 10.07	1.25	0.298
Snout to snout contact	14.43 \pm 3.23	11.77 \pm 4.03	0.19	0.665	8.83 \pm 4.28	14.50 \pm 3.63	15.55 \pm 2.86	0.08	0.922	9.63 \pm 4.36	15.11 \pm 3.37	2.29	0.299	11.29 \pm 3.27	14.16 \pm 3.41	12.79 \pm 3.01	0.04	0.962
Other	25.63 \pm 5.20	21.83 \pm 6.03	0.00	0.994	13.90 \pm 7.06	26.12 \pm 6.64	28.49 \pm 4.99	0.62	0.543	16.16 \pm 6.44	28.47 \pm 5.01	1.27	0.331	22.34 \pm 5.19	20.06 \pm 5.11	26.91 \pm 5.52	2.84	0.071

Abbreviations: PSE, prior stall experience; BCS, body condition score; PTE, prior training experience.

Table A.3. Percentage of time (mean \pm SEM) spent in locomotion, exploratory behaviour and snout to snout contact and in other behaviours by sows from the high score population (sows that reached a minimum FR of 72; n = 10) with regard to the FR. The non-transformed (raw) mean and SEM values are presented.

Behaviour type	FR									F-value	P-value
	9	14	21	32	48	72	108	162	243		
Locomotion	14.94 \pm 2.34	15.91 \pm 2.36	14.28 \pm 2.34	12.14 \pm 2.36	14.09 \pm 2.40	12.21 \pm 2.55	13.76 \pm 3.98	18.43 \pm 6.45	12.41 \pm 9.15	0.37	0.931
Exploratory behaviour	38.22 \pm 10.12	44.53 \pm 10.15	44.20 \pm 10.12	52.72 \pm 10.15	50.82 \pm 10.19	53.11 \pm 10.44	65.57 \pm 12.84	54.73 \pm 15.53	84.35 \pm 23.47	1.82	0.094
Snout to snout contact	9.91 \pm 3.86	11.24 \pm 3.88	12.07 \pm 3.86	15.56 \pm 3.88	17.77 \pm 3.91	11.41 \pm 4.08	8.54 \pm 5.88	5.75 \pm 9.41	7.61 \pm 14.52	0.53	0.825
Other	34.01 \pm 6.30	24.81 \pm 6.38	23.75 \pm 6.35	16.21 \pm 6.38	14.08 \pm 6.46	18.89 \pm 7.05	7.50 \pm 11.04	16.17 \pm 15.29	0.77 \pm 24.38	1.33	0.251

Abbreviations: FR, fixed ratio.

Table A.4. Percentage of time (mean \pm SEM) spent in locomotion, exploratory behaviour, snout to snout contact and in other behaviours by sows from the low score population (sows that reached the maximum FR of 48; n = 14) with regard to the PTE and FR. The non-transformed (raw) mean and SEM values are presented.

Behaviour type	PTE				FR						
	Exercise first	Feed first	F-value	P-value	9	14	21	32	48	F-value	P-value
Locomotion	18.81 \pm 4.64	13.38 \pm 4.11	0.51	0.521	15.42 \pm 3.25	15.43 \pm 3.34	14.60 \pm 3.40	14.16 \pm 3.66	20.87 \pm 4.51	0.86	0.500
Exploratory behaviour	43.71 \pm 11.93	39.73 \pm 9.78	0.06	0.819	36.28 \pm 8.15	39.17 \pm 8.37	47.99 \pm 8.71	47.30 \pm 9.65	37.86 \pm 12.78	0.99	0.431
Snout to snout contact	6.71 \pm 6.92	23.77 \pm 5.88	3.97	0.117	13.11 \pm 4.83	10.51 \pm 5.02	10.92 \pm 5.23	21.21 \pm 5.67	20.43 \pm 7.66	1.44	0.241
Other	31.07 \pm 14.04	17.37 \pm 12.04	0.71	0.459	33.99 \pm 9.56	33.82 \pm 9.77	24.97 \pm 10.02	14.87 \pm 10.68	13.44 \pm 13.03	2.20	0.097

Abbreviations: PTE, prior training experience; FR, fixed ratio.

Table A.5. Percentage of time (mean \pm SEM) spent in locomotion, exploratory behaviour and snout to snout contact and in other behaviours by sows from the high score population (sows that reached a minimum FR of 72; n = 10) with regard to the FR at each opportunity number. The non-transformed (raw) mean and SEM values are presented.

Opportunity number	FR									F-value	P-value
	9	14	21	32	48	72	108	162	243		
	<i>Locomotion</i>									1.15	0.337
1	18.25 \pm 2.69	20.29 \pm 2.69	18.10 \pm 2.69	16.76 \pm 2.69	17.10 \pm 2.69	13.16 \pm 2.69	12.62 \pm 3.35	13.54 \pm 5.62	7.44 \pm 7.97		
2	11.83 \pm 3.75	18.69 \pm 3.75	14.14 \pm 3.75	10.62 \pm 3.75	16.69 \pm 3.92	10.98 \pm 3.92	10.91 \pm 7.77	20.21 \pm 8.11	-		
3	14.73 \pm 2.71	8.76 \pm 2.84	10.60 \pm 2.71	9.05 \pm 2.84	8.47 \pm 2.84	12.48 \pm 3.77	17.75 \pm 5.70	-	-		
	<i>Exploratory behaviour</i>									0.94	0.521
1	39.87 \pm 8.55	40.92 \pm 8.55	46.60 \pm 8.55	51.18 \pm 8.55	54.90 \pm 8.55	53.16 \pm 8.55	58.79 \pm 10.16	58.03 \pm 16.12	84.40 \pm 22.49		
2	51.34 \pm 8.51	48.06 \pm 8.51	51.04 \pm 8.51	53.68 \pm 8.51	61.40 \pm 8.81	65.44 \pm 8.81	79.06 \pm 15.80	57.95 \pm 16.08	-		
3	37.10 \pm 8.99	58.23 \pm 9.31	48.57 \pm 8.99	66.81 \pm 9.31	49.65 \pm 9.34	55.91 \pm 11.64	66.99 \pm 17.38	-	-		
	<i>Snout to snout contact</i>									0.57	0.872
1	9.22 \pm 4.87	10.43 \pm 4.87	12.18 \pm 4.87	15.01 \pm 4.87	17.14 \pm 4.87	15.37 \pm 4.87	8.94 \pm 5.98	5.92 \pm 9.95	7.37 \pm 14.60		
2	12.91 \pm 5.57	9.69 \pm 5.57	11.60 \pm 5.57	20.22 \pm 5.57	16.79 \pm 5.77	11.43 \pm 5.80	7.83 \pm 10.69	7.76 \pm 12.03	-		
3	7.59 \pm 4.36	13.61 \pm 4.50	12.44 \pm 4.36	11.46 \pm 4.52	19.38 \pm 4.54	7.41 \pm 5.68	8.85 \pm 8.49	-	-		
	<i>Other</i>									0.66	0.797
1	34.29 \pm 7.93	29.98 \pm 7.93	24.75 \pm 7.93	18.67 \pm 7.93	12.49 \pm 7.93	19.93 \pm 7.93	22.00 \pm 10.18	22.80 \pm 17.57	0.51 \pm 25.15		
2	25.54 \pm 7.67	25.18 \pm 7.67	16.48 \pm 8.02	17.11 \pm 7.67	5.97 \pm 8.03	13.01 \pm 8.02	0.12 \pm 16.07	11.88 \pm 16.90	-		
3	42.21 \pm 9.24	19.28 \pm 9.73	30.02 \pm 9.24	12.83 \pm 9.71	23.80 \pm 9.72	23.72 \pm 12.88	0.63 \pm 20.21	-	-		

Abbreviations: FR, fixed ratio.

Table A.6. Percentage of time (mean \pm SEM) spent in locomotion, exploratory behaviour, snout to snout contact and in other behaviours by sows from the low score population (sows that reached the maximum FR of 48; n = 14) with regard to the FR at each opportunity number. The non-transformed (raw) mean and SEM values are presented.

Opportunity number	FR					F-value	P-value
	9	14	21	32	48		
	<i>Locomotion</i>					0.84	0.573
1	17.39 \pm 3.65	17.34 \pm 3.74	19.83 \pm 3.80	16.89 \pm 3.92	21.98 \pm 4.83		
2	15.60 \pm 3.52	16.67 \pm 3.65	14.81 \pm 3.75	13.50 \pm 4.49	15.17 \pm 6.06		
3	13.26 \pm 3.34	12.28 \pm 3.49	9.16 \pm 3.76	12.07 \pm 4.15	25.48 \pm 6.20		
	<i>Exploratory behaviour</i>					0.57	0.797
1	24.08 \pm 9.05	28.63 \pm 9.22	28.64 \pm 9.42	38.48 \pm 9.74	30.53 \pm 11.74		
2	42.03 \pm 9.86	42.69 \pm 10.17	50.21 \pm 10.64	48.08 \pm 13.00	41.49 \pm 18.44		
3	42.74 \pm 9.42	46.20 \pm 9.88	65.14 \pm 11.10	55.33 \pm 13.08	41.55 \pm 21.31		
	<i>Snout to snout contact</i>					1.22	0.309
1	8.96 \pm 5.33	7.49 \pm 5.48	12.29 \pm 5.58	15.57 \pm 5.80	11.22 \pm 7.31		
2	12.98 \pm 5.54	10.65 \pm 5.80	16.43 \pm 6.03	19.74 \pm 7.42	29.43 \pm 10.49		
3	17.39 \pm 5.67	13.39 \pm 6.08	4.05 \pm 7.10	28.30 \pm 8.19	20.65 \pm 14.37		
	<i>Other</i>					0.81	0.601
1	48.05 \pm 11.07	45.41 \pm 11.28	38.94 \pm 11.50	29.17 \pm 11.86	35.62 \pm 14.33		
2	27.86 \pm 10.51	29.22 \pm 10.77	17.38 \pm 11.08	17.65 \pm 12.71	16.02 \pm 16.74		
3	26.06 \pm 10.31	26.84 \pm 10.74	18.60 \pm 11.70	2.22 \pm 13.25	11.31 \pm 20.03		

Abbreviations: FR, fixed ratio.

APPENDIX B

Table B.1. Percentage of time (mean \pm SEM) spent in locomotion, exploratory behaviour, snout to snout contact and in other behaviours by sows from the high score population (sows that reached a minimum FR of 72; n = 15), belonging to one of three treatments: sows receiving 50% of their ad-lib high fibre feed intake (0.5 HF), sows fed high fibre feed ad-lib (ad-lib HF) and control sows receiving no high fibre feed additional to their standard ration (C) with regard to treatment, parity, opportunity number and BCS. The non-transformed (raw) mean and SEM values are presented. Where superscripts differ, $P < 0.05$. * Tendency: $P < 0.10$.

Behaviour type	Treatment					Parity						Opportunity number						BCS			
	C	0.5 HF	ad-lib HF	F-value	P-value	2	3	4	5	F-value	P-value	1	2	3	F-value	P-value	2	3	4	F-value	P-value
	N																				
	7	5	3			5	6	4	0			15	15	15			2	11	2		
Loco-motion	12.93 \pm 2.08	15.33 \pm 2.38	12.49 \pm 2.34	0.88	0.422	15.27 \pm 2.49	13.08 \pm 1.89	12.41 \pm 2.24	-	0.78	0.465	16.85 \pm 1.78 ^a	13.72 \pm 1.90 ^b	10.18 \pm 1.90 ^c	12.39	< 0.001	13.60 \pm 3.00	13.25 \pm 1.54	13.90 \pm 3.17	0.04	0.959
Exploratory behaviour	55.27 \pm 8.48 ^{a*}	71.19 \pm 9.41 ^{b*}	68.08 \pm 9.72 ^{ab*}	3.18	0.052	65.43 \pm 9.92	77.63 \pm 10.32	51.48 \pm 10.96	-	1.13	0.347	59.56 \pm 8.06	67.46 \pm 8.29	67.52 \pm 8.57	1.11	0.340	80.85 \pm 13.51	60.30 \pm 8.25	53.40 \pm 10.61	1.23	0.305
Snout to snout contact	10.12 \pm 0.88	7.70 \pm 1.13	14.37 \pm 2.12	1.27	0.289	12.47 \pm 1.41	6.85 \pm 0.72	13.22 \pm 1.73	-	1.29	0.283	9.57 \pm 1.08	9.40 \pm 1.09	12.00 \pm 1.61	0.41	0.668	6.17 \pm 1.27 ^{a*}	11.49 \pm 0.87 ^{b*}	6.89 \pm 1.97 ^{ab*}	2.44	0.096
Other	18.02 \pm 6.20 ^a	6.84 \pm 6.98 ^b	13.21 \pm 7.11 ^{ab}	3.59	0.036	14.70 \pm 7.48	10.63 \pm 7.12	12.73 \pm 7.72	-	0.41	0.666	15.61 \pm 5.74 ^{a*}	10.62 \pm 5.98 ^{b*}	11.83 \pm 6.34 ^{b*}	3.11	0.056	8.12 \pm 10.07	12.40 \pm 5.69	17.55 \pm 8.25	1.20	0.314

Abbreviations: BCS, body condition score.

Table B.2. Percentage of time (mean \pm SEM) spent in locomotion, exploratory behaviour, snout to snout contact and in other behaviours by sows from the low score population (sows that reached the maximum FR of 48; n = 27) with regard to FR and BCS. The non-transformed (raw) mean and SEM values are presented. Where superscripts differ, $P < 0.05$. *Tendency: $P < 0.10$.

Behaviour	FR					F-value	P-value	BCS					F-value	P-value
	9	14	21	32	48			2	3	4				
	N													
	27	22	20	16	9			2	20	5				
Loco- motion	17.79 ± 2.21	17.47 ± 2.31	15.63 ± 2.37	15.66 ± 2.63	14.64 ± 3.44	0.80	0.526	14.73 ± 3.93	17.05 ± 2.15	16.93 ± 2.90	0.25	0.783		
Explorato- ry behaviour	47.62 ± 6.35	43.84 ± 6.72	48.77 ± 6.96	48.84 ± 7.60	51.09 ± 9.36	0.26	0.902	51.77 ± 11.36	44.43 ± 5.86	47.90 ± 8.33	0.09	0.917		
Snout to snout contact	10.37 ± 3.55	10.88 ± 3.67	13.66 ± 3.77	16.20 ± 4.00	16.65 ± 4.67	1.20	0.317	7.90 ± 6.14 ^a	22.20 ± 3.40 ^b	10.56 ± 4.61 ^a	7.69	0.001		
Other	23.95 ± 4.01	26.76 ± 4.40	20.64 ± 4.59	18.25 ± 5.32	18.74 ± 7.52	0.48	0.750	26.55 ± 7.69	16.76 ± 3.78	21.70 ± 5.63	0.77	0.472		

Abbreviations: FR, fixed ratio; BCS, body condition score.

APPENDIX C

Table C.1. Relative frequency (mean \pm SEM) of lying, sitting and standing during the AM and PM data collection periods for sows stall-housed throughout the gestation (Control, n = 53), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, n = 56) and sows housed in groups from insemination to farrowing (Group, n = 58) in early (week 2), mid (week 10) and late gestation (week 15). The non-transformed (raw) mean and SEM values are presented. The values with different superscript letters are significantly different ($P \leq 0.05$), asterisks indicate tendency ($P < 0.1$).

Posture	Stage of gestation									F-value	P-value
	Early			Mid			Late				
	Treatment										
	C	E	G	C	E	G	C	E	G		
	N										
	53	56	58	53	56	58	53	56	58		
<i>AM</i>											
Lying	0.37 ± 0.05	0.34 ± 0.05	0.52 ± 0.05	0.41 ± 0.05	0.51 ± 0.05	0.51 ± 0.05	0.55 ± 0.05	0.63 ± 0.05	0.72 ± 0.05	1.73	0.143
Sitting	0.12 ± 0.03	0.13 ± 0.03	0.06 ± 0.03	0.15 ± 0.03	0.19 ± 0.03	0.10 ± 0.03	0.17 ± 0.03	0.15 ± 0.03	0.13 ± 0.03	1.06	0.377
Standing	0.46 ± 0.04 ^{a*}	0.54 ± 0.04 ^{b*}	0.42 ± 0.04 ^{a*}	0.43 ± 0.04 ^{a*}	0.30 ± 0.04 ^{b*}	0.37 ± 0.04 ^{ab*}	0.28 ± 0.05 ^a	0.23 ± 0.04 ^{ab}	0.12 ± 0.05 ^b	2.71	0.030
<i>PM</i>											
Lying	0.59 ± 0.05	0.62 ± 0.05	0.59 ± 0.05	0.69 ± 0.05	0.64 ± 0.05	0.72 ± 0.05	0.74 ± 0.05	0.75 ± 0.05	0.76 ± 0.05	0.49	0.740
Sitting	0.08 ± 0.02	0.10 ± 0.02	0.03 ± 0.02	0.08 ± 0.02	0.14 ± 0.02	0.04 ± 0.02	0.09 ± 0.02	0.12 ± 0.02	0.06 ± 0.02	0.46	0.766
Standing	0.26 ± 0.04	0.26 ± 0.04	0.32 ± 0.04	0.21 ± 0.04	0.22 ± 0.04	0.20 ± 0.04	0.18 ± 0.04	0.13 ± 0.04	0.16 ± 0.04	0.84	0.498

Abbreviations: C, control; E, exercise; G, group.

Table C.2. Relative frequency (mean \pm SEM) of lying, sitting and standing during the PM data collection period for sows stall-housed throughout the gestation (Control, n = 53), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, n = 56) and sows housed in groups from insemination to farrowing (Group, n = 58) in early (week 2), mid (week 10) and late gestation (week 15). The non-transformed (raw) mean and SEM values are presented. The values with different superscript letters are significantly different ($P \leq 0.05$), asterisks indicate tendency ($P < 0.1$).

Posture	Treatment			F-value	P-value	Stage of gestation			F-value	P-value
	C	E	G			Early	Mid	Late		
	N									
	53	56	58			167	167	167		
Lying	0.67 \pm 0.04	0.67 \pm 0.04	0.69 \pm 0.04	0.14	0.867	0.60 \pm 0.04 ^a	0.68 \pm 0.03 ^{b*}	0.75 \pm 0.04 ^{c*}	7.40	0.001
Sitting	0.15 \pm 0.02 ^a	0.16 \pm 0.02 ^b	0.10 \pm 0.02 ^c	10.93	< 0.001	0.10 \pm 0.02	0.15 \pm 0.02	0.15 \pm 0.02	0.94	0.392
Standing	0.22 \pm 0.3	0.21 \pm 0.03	0.23 \pm 0.03	0.44	0.641	0.28 \pm 0.03 ^a	0.21 \pm 0.03 ^a	0.16 \pm 0.03 ^b	5.84	0.003

Abbreviations: C, control; E, exercise; G, group.

Table C.3. Relative frequency (mean \pm SEM) of performing stereotypies (a total of sham chewing, bar-biting, tongue-rolling and trough manipulation) during the PM data collection period for sows stall-housed throughout the gestation (Control, n = 53), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, n = 56) and sows housed in groups from insemination to farrowing (Group, n = 58) in early (week 2), mid (week 10) and late gestation (week 15). The non-transformed (raw) mean and SEM values are presented. $F_{4,459} = 1$; $P = 0.136$.

Stage of gestation	Treatment					
	C		E		G	
	N					
	53		56		58	
	Mean	SEM	Mean	SEM	Mean	SEM
Early	0.32	0.05	0.37	0.05	0.21	0.05
Mid	0.47	0.05	0.50	0.05	0.31	0.05
Late	0.36	0.05	0.33	0.05	0.35	0.05

Abbreviations: C, control; E, exercise; G, group.

Table C.4. Results of the novel object tests in piglets (n = 168, 3 piglets per sow from 54 sows and 2 piglets per sow from 3 sows), born from sows stall-housed throughout the gestation (Control, n = 17), stall-housed sows walked for 160 m around the gestation room once per week (Exercise, n = 20) and sows housed in groups from insemination to farrowing (Group, n = 20), belonging to young (parity 0-1; n = 14), mid (parity 2-4, n = 34), and old (parity 5-7, n = 9) parity groups (mean \pm SEM). The non-transformed (raw) mean and SEM values are presented. The values with different superscript letters are significantly different ($P \leq 0.05$), asterisks indicate tendency ($P < 0.1$).

Variable	Young (n = 14)		Mid (n = 34)		Old (n =9)		F-value	P-value
	Mean	SEM	Mean	SEM	Mean	SEM		
Number of squares visited	19.42	2.49	20.43	1.79	19.52	2.80	0.10	0.909
Number of vocalizations	58.44	7.92	52.57	5.92	55.57	8.82	0.59	0.554
Frequency of entering the 1.00 m circle	4.30	0.56	4.33	0.35	4.63	0.66	0.47	0.629
Frequency of entering the 0.50 m circle	2.10	0.32	2.10	0.21	2.30	0.36	0.08	0.925
Frequency of exiting the 1.00 m circle and remaining in the area bordering the perimeter of the pen	2.10	0.32	2.19	0.21	2.44	0.36	0.53	0.589
Latency to enter the 1.00 m circle (s)	39.76 ^{a*}	8.45	41.66 ^{a*}	5.65	28.41 ^{b*}	9.64	2.41	0.095
Latency to enter the 0.50 m circle (s)	50.13	9.00	52.62	6.35	41.86	10.14	1.17	0.312
Latency to touch the novel object (s)	52.69	8.98	56.13	6.42	49.22	10.08	0.86	0.428
Number of contacts with the novel object	2.57	0.53	2.81	0.41	2.34	0.58	0.06	0.940