ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

SLU

DOCTORAL THESIS NO. 2026:24
FACULTY OF VETERINARY MEDICINE AND ANIMAL SCIENCES

You reap what you sow

Effects of early social environments and genetic line on behaviour and welfare indicators in sow group housing

LINDA MARIE BACKEMAN HANNIUS

You reap what you sow

Effects of early social environments and genetic line on behaviour and welfare indicators in sow group housing

Linda Marie Backeman Hannius
Faculty of Veterinary Medicine and Animal Sciences
Department of Applied Animal Science and Welfare
Uppsala

SLU
SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS
Uppsala 2026

Acta Universitatis Agriculturae Sueciae
2026:24

Cover: Original watercolour painting of sows in straw by Anna Lundberg, 2026.

ISSN 1652-6880
ISBN (print version) 978-91-8124-241-6
ISBN (electronic version) 978-91-8124-271-3
https://doi.org/10.54612/a.3q29jgrnfv

Swedish University of Agricultural Sciences, Department of Applied Animal Science and Welfare, Uppsala, Sweden

Print: SLU Grafisk service, Uppsala 2026

You reap what you sow

Effects of early social environments and genetic line on behaviour and welfare indicators in sow group housing systems

Abstract

Social interactions in group-housed pigs have important consequences for animal welfare, yet individuals differ substantially in their behavioural expressions and responses to social challenges. This thesis investigated how early social environments and genetic line influence behavioural development, social responses and welfare-related outcomes in group-housed gilts and sows.

Across a series of experimental studies, gilts from two genetic lines were followed from early rearing throughout gilt development and into first parity, with variation in social experience created by early and late social mixing treatments. The behaviour of individuals post-weaning, including activity, pen use and social interactions, was assessed, and later-life responses to unfamiliar conspecifics were evaluated in standardised paired interaction tests together with lesion outcomes to indicate the intensity of social challenges. An observational study in commercial herds described the prevalence and distribution of lesions, lameness and body soiling under practical production conditions.

Early social experience, in which piglets were mixed with a litter from a neighbouring pen during lactation, influenced behavioural expression after weaning and later influenced how females responded to social challenges, but did not consistently reduce aggression. Later social experience, involving regrouping with unfamiliar individuals after weaning, modified aspects of behavioural strategy during paired interactions. Genetic line was repeatedly associated with the type of initiated social behaviour, with response patterns and lesion outcomes indicating line-specific differences in social behaviour expressed across life stages and varying by social interaction type. Variation in welfare-related outcomes observed in commercial herds further demonstrated that lesion occurrence and other indicators varied with production stage and management conditions.

In conclusion, social behaviour and welfare-related outcomes in group-housed breeding females reflect the combined effects of genetic background and social experience across life stages. The findings highlight the importance of considering how individuals initiate, respond to and regulate social interactions when evaluating welfare in systems characterised by repeated social mixing and provide relevant knowledge for assessing and developing management practices in modern pig production.

Keywords: pig, gilt, sow, social behaviour, group housing, social experience, genetic line, behavioural strategies, animal welfare, lesions

You reap what you sow

Effekter av tidig social erfarenhet och genetisk linje på beteende och välfärdsindikatorer hos suggor i grupphållning

Sammanfattning

Sociala interaktioner hos grupphållna grisar har stor betydelse för djurvälfärden, men individer skiljer sig i sitt beteendeuttryck och i sina responser på sociala utmaningar. Sådana skillnader kan uppstå tidigt i livet och återspegla både social erfarenhet och genetisk bakgrund. Syftet med denna avhandling var att undersöka hur tidig social erfarenhet och genetisk linje påverkar beteendeutveckling, sociala responser och välfärdsrelaterade utfall hos grupphållna gyltor och suggor.

I en serie experimentella studier studerades gyltor från två olika avelslinjer från tidig uppfödning fram till första grisningen. Beteendeförändringar efter avvänjning studerades, och vid flera olika åldrar undersöktes grisarnas responser vid standardiserade möten med obekanta artfränder. När de avvant sin första kull registrerades även sår som en indikatorer på de sociala interaktionernas konsekvenser. Resultaten från de experimentella studierna kompletterades med en observationsstudie i kommersiella besättningar, där förekomst och fördelning av sår, hälta och nedsmutsning kartlades.

Tidig social erfarenhet påverkade beteende efter avvänjning och återspeglades även i hur de svarade på sociala utmaningar senare i livet. Dock ledde tidig social erfarenhet inte konsekvent till minskad aggression. Erfarenhet av blandning med okända individer var relaterat till förändrade beteendestrategier under sociala interaktioner. Avelslinje var på flera sätt relaterat till typ av initierade beteenden i sociala interaktioner, responsmönster och sårförekomst, vilket indikerar linjespecifika mönster i socialt beteende som uttrycktes i olika sammanhang. Den variation i förekomst av välfärdsindikationer som observerades i kommersiella besättningar förstärkte bilden av att sårförekomst och andra indikatorer är kontextberoende och påverkas av hur djuren hålls och hanteras.

Sammanfattningsvis påverkas socialt beteende och förekomst av välfärdsindikatorer hos grupphållna gyltor och suggor i olika stadier i livet av grisarnas genetiska bakgrund och sociala erfarenhet. Förbättrad välfärd i grupphållning handlar därför inte enbart om att minska skador, utan också om att skapa förutsättningar för suggor att hantera de sociala utmaningar som uppstår i moderna produktionssystem.

Nyckelord: gris, gylta, sugga, socialt beteende, grupphållning, social erfarenhet, genetisk linje, beteendestrategier, djurvälfärd, sår

You reap what you sow

Varajase sotsiaalse keskkonna ja geneetilise tausta mõju rühmapidamisel peetavate emiste käitumisele ja heaolunäitajatele

Kokkuvõte

Rühmas peetavate sigade sotsiaalsed suhted mõjutavad oluliselt nende heaolu. Samas käituvad loomad erinevalt – mõned tulevad sotsiaalsete olukordadega paremini toime kui teised. Need erinevused võivad kujuneda juba varases elus ning olla seotud nii loomade varasemate sotsiaalsete kogemuste kui ka geneetilise taustaga. Käesolevas doktoritöös uuriti, kuidas varajane sotsiaalne keskkond ja geneetiline liin mõjutavad käitumise kujunemist, sotsiaalseid reaktsioone ja heaoluga seotud näitajaid rühmas peetavatel noorsigadel ja emistel.

Uuringutes jälgiti kahe erineva geneetilise liini noorsigu alates varasest üleskasvamisest kuni esimese poegimiseni. Võõrutamise järgselt hinnati loomade aktiivsust, ruumikasutust ja sotsiaalseid suhteid. Hilisemas eas uuriti, kuidas nad reageerisid tundmatutele liigikaaslastele standardiseeritud paaristestides ning hinnati ka vigastusi kui sotsiaalsete olukordade intensiivsuse näitajaid. Lisaks viidi läbi vaatlusuuring tootmisfarmides, kus kirjeldati vigastuste, lonkamise ja määrdumise esinemist tavapärastes tootmistingimustes.

Tulemused näitasid, et sotsiaalne kogemus mõjutas loomade käitumist juba pärast võõrutamist ning need erinevused avaldusid ka hilisemates sotsiaalsetes olukordades. Varajane põrsaste rühmitamine ei vähendanud siiski alati agressiivsust, vaid mõjutas pigem seda, milliseid erinevaid käitumisstrateegiaid loomad sotsiaalsetes olukordades kasutasid.Samuti ilmnes erinevusi käitumises ja vigastuste esinemises erinevate geneetiliste liinide vahel. Tootmisfarmides täheldatud suur varieeruvus heaolunäitajates rõhutas, et loomade heaolu kujuneb nii individuaalse käitumise kui ka pidamistingimuste ja majandamisviisi koosmõjul.

Kokkuvõttes näitab see töö, et rühmas peetavate aretusemasloomade sotsiaalne käitumine ja heaoluga seotud näitajad kujunevad aja jooksul geneetilise tausta ja varajaste kogemuste koosmõjul. Loomade individuaalsete erinevuste arvestamine on oluline, kui hinnatakse heaolu ja arendatakse pidamis- ja majandamispraktikaid süsteemides, kus loomi korduvalt ümber rühmitatakse.

Võtmesõnad: siga, põrsas, emis, sotsiaalne käitumine, rühmapidamine, sotsiaalne kogemus, geneetiline liin, käitumisstrateegiad, loomade heaolu, vigastused

Preface

Modern pig production is shaped by a fundamental tension. On the one hand, pigs are socially and cognitively complex animals, capable of flexible behaviour, learning and adaptation. On the other hand, they are managed within production systems that must remain economically viable and practically feasible for farmers over time. Reconciling these realities is one of the central challenges for animal welfare research today, and it forms the broader motivation for this thesis.

The work brought together in this thesis is grounded in the view that indicators of welfare cannot be reduced to isolated measures or short-term outcomes. Social behaviour, in particular, emerges through interactions between individual predispositions, including genetic background and early-life experiences, and the social and physical environments encountered across life. Understanding these processes requires perspectives that extend beyond single experiments or production stages, and that acknowledge both the benefits and the costs inherent to social living.

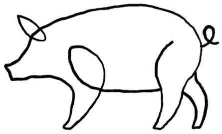
The purpose of this thesis is to provide a coherent structure for reading and integrating the individual studies conducted within this PhD project. Rather than repeating the content of the papers, it synthesises their contributions and places them in a broader context, connecting findings across life stages and research settings that span both experimental and commercial production environments.

This thesis aims to contribute to a way of thinking about social behaviour that emphasises responsiveness, context and cumulative experience as opposed to single expressions of e.g. aggression or affiliation. Social strategies are understood as situational and dynamic, shaped by both past and present conditions, and potentially associated with trade-offs that are relevant for welfare over the long term.

Ultimately, improving welfare in pig production is not only a question of optimising environments or considering the behavioural complexity of pigs. It also concerns sustainability: developing systems that are defensible over time for animals, farmers and society. This thesis adopts the perspective that meaningful progress lies in aligning animals, management, and environments, placing the right animals in the right environment, whilst also recognising the complexity of the animals we work with and the realities of the systems in which they are kept.

Dedication

Till Leia, en påminnelse om att alla variabler inte kan kontrolleras. ♡



If pigs were simple, this thesis would be shorter.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Hannius, L. M. B., Keeling, L., Ask-Gullstrand, P., Verbeek, E., & Wallenbeck, A. (2023). Effects of early social mixing and genetic line on female piglet activity, pen location and social interactions pre- and post-weaning under Swedish commercial pig production conditions. *Acta Agriculturae Scandinavica, Section A — Animal Science*, 72(3–4), 135–148. https://doi.org/10.1080/09064702.2023.2245416

II. Backeman Hannius, L. M., Keeling, L., de Oliveira, D., Anderson, C., & Wallenbeck, A. (2024). Friend or foe: effects of social experience and genetic line on responses of young gilts in a social challenge paired interaction test. *Animal*, 18(11), 101349. https://doi.org/10.1016/j.animal.2024.101349

III. Backeman Hannius, L. M., Keeling, L. & Wallenbeck, A. (2025) Under pressure: effect of first-parity sows' early social experience and genetic line on behavior and lesions in a paired interaction test with an older sow. *Frontiers in Animal Science*, 6:1711609. https://doi.org/10.3389/fanim.2025.1711609

IV. Anderson, C., Backeman Hannius, L. M., de Oliveira, D. & Wallenbeck, A. (2024). Social sham chewing in sows? *Behavioural Processes*, 218:105042. https://doi.org/10.1016/j.beproc.2024.105042

V. Backeman Hannius, L. M., Carlzén, H., Westin, R. & Wallenbeck, A. Marks of conflict: A cross-sectional study of skin lesions, lameness and body soiling in group-housed sows and gilts during mating and gestation in Swedish commercial piglet-producing farms (manuscript).

All published papers are reproduced with the permission of the publisher or published open access.

The contribution of Linda Marie Backeman Hannius to the papers included in this thesis was as follows:

I. Main author. Developed the research aims and conceptual framework, designed the methodology, conducted the investigation and curated the data. Performed formal statistical analyses and data visualisation. Coordinated project administration. Drafted and led the writing of the manuscript, including revision and editing in collaboration with co-authors.

II. Main author. Developed the research aims and conceptual framework and contributed to the methodological design. Conducted the investigation and curated the data. Performed formal statistical analyses, including the development and application of analytical software, and contributed to the validation of the results. Led the data visualisation. Drafted and led the writing of the manuscript, including substantial revision and editing in collaboration with co-authors.

III. Main author. Developed the research aims and conceptual framework, designed the methodology and conducted the investigation. Curated and validated the data, developed and applied analytical software, and performed formal statistical analyses. Led the data visualisation. Drafted and led the writing of the manuscript, including critical revision and editing in collaboration with co-authors.

IV. Co-author with a major contribution. Contributed to the development of the research aims and conceptual framework, methodology and investigation. Participated in data curation and contributed to the critical review and editing of the manuscript.

V. Main author. Led the conceptualisation of the study and development of the methodology, including software implementation. Conducted the investigation, data curation, formal analysis and validation of results. Prepared figures and visualisations, and drafted and led the writing of the manuscript, including revision and editing in collaboration with co-authors.

List of tables

List of figures

Abbreviations

SY	Swedish Yorkshire
DY	Dutch Yorkshire
AP	Access pen
CP	Conventional/Closed pen
MG	Mixed group
IG	Intact group
FPS	First parity sow

Abbreviations related to legislation

BEK nr 15, 2026	Styrelsen for Fødevarer, Landbrug og Fiskeri. Bekendtgørelse om dyrevelfærdsmæssige mindstekrav til hold af grise (BEK nr 15 af 8. januar 2026). Retsinformation. [Danish executive order on minimum animal welfare requirements for the keeping of pigs].
Besluit houders van dieren, 2026	Government of the Netherlands. Besluit houders van dieren. Staatsblad van het Koninkrijk der Nederlanden. Available at: https://wetten.overheid.nl/BWBR0035217/ (accessed 19 January 2026).
Dir 2008/120/EC	Council Directive 2008/120/EC of 18 December 2008 laying down minimum standards for the protection of pigs.
SJVFS 2019:20 (L106)	Statens jordbruksverks föreskrifter och allmänna råd (SJVFS 2019:20) om grishållning inom lantbruket m.m., saknr L106 [Swedish Board of Agriculture regulations and general recommendations (SJVFS 2019:20) on pig husbandry in agriculture, Case No. L106.]
Swedish Animal Welfare Ordinance, (1988:539) or (2019:66)	Animal Welfare Ordinance (2019:66) (previously: 1988:539), Swedish Code of Statutes.

1. Introduction

The phrase "you reap what you sow" has long been used in societal and cultural contexts to capture the idea that choices shape future outcomes. In agriculture, it carries both a literal and metaphorical meaning: the seeds planted and the care invested early on determine the harvest that follows. Applied more broadly, it reflects the principle that investments now lead to returns later. In pig production, this principle can be understood as the long-term consequences of early-life management, social experience and genetic background regarding how gilts and sows cope with the demands later in life, e.g. group housing. Although such effects are not always linear or predictable, the metaphor highlights the importance of considering early conditions as part of the foundation for later welfare, social functioning and performance.

Against this background, this thesis examines how early-life social experience and genetic background shape certain aspects of behavioural development and welfare-related outcomes in group-housed gilts and sows. Across a series of experimental studies following the same individuals from early rearing into first parity (Papers I–IV), behavioural development, responses to unfamiliar conspecifics in standardised social challenges and short-term lesion outcomes were assessed. These assessments are complemented with an observational study in commercial Swedish herds (Paper V), describing the prevalence and distribution of lesions, lameness and body soiling under group-housing conditions in commercial piglet production. Together, the work aims to clarify what is '*sown*' early in life and what may later be '*reaped*' in terms of behavioural patterns, social functioning and welfare-related indicators in modern sow group-housing systems.

2. Background

Pigs are socially complex animals whose behaviour and welfare are shaped by their interactions with both conspecifics and their environment. In commercial production systems, these biological characteristics interact with management routines, housing design and economic constraints. Thus, welfare outcomes reflect the combined effects of animal characteristics and production conditions, rather than a single cause. Understanding the welfare of group-housed gilts and sows therefore requires consideration of both biological and production-related conditions. The following chapter outlines the societal, legislative, biological and production conditions that are relevant for welfare outcomes in group-housed gilts and sows.

2.1 Animal welfare

2.1.1 Legislation and societal expectations

The welfare of farm animals has increasingly grown into both a political and societal concern, reflected in regulatory frameworks and consumer expectations. Within pig production, sow housing has been a central aspect of this development in recent decades. Sweden was one of the first countries to prohibit sow stalls, through legislation introduced in 1988 (Swedish Animal Welfare Ordinance, 1988:539), which established loose housing as the standard housing system for sows throughout their reproductive cycle. Importantly, Swedish legislation also mandates group housing during the entire gestation period (SJVFS 2019:20 (L106)), meaning that sows are kept in groups from weaning throughout the mating and gestation period until they are moved to farrowing pens to give birth to their next litter. Around farrowing and lactation, sows are housed individually in loose-housed farrowing pens, but without fixation, which was banned in Sweden from 1994 (SJVFS 2019:20 (L106)). In contrast, the European Union Directive (Dir 2008/120/EC, Article 3.4) stipulates that from 2013 onwards, gilts and sows must be group housed, but only from four weeks after mating (or insemination) until one week before farrowing. Thus, individual stalls during mating and early gestation as well as farrowing crates during farrowing and lactation can be used. Compared to the EU regulations for pigs (Dir 2008/120/EC), Swedish legislation entails a more extensive application of group housing across a greater part of the reproductive cycle, thereby enabling gilts and sows to socially interact across a larger proportion of their lives.

Beyond the legal requirements, consumer expectations and public debate have strongly influenced the development of pig production. Societal concern has expanded beyond the prevention of suffering to include opportunities for animals to express natural behaviours and to experience positive welfare (Rault *et al.*, 2022). In the EU this is reflected in the European Citizens' Initiative '*End the Cage Age*', which includes suggestions to prohibit farrowing crates for sows and sow stalls, where not already prohibited (European Citizens' Initiative, 2025). In Sweden, where animal welfare legislation is considered to be stricter compared to most other countries, these expectations have become an important part of the pig industry's identity and market competitiveness. At the same time, high welfare standards place additional demands on producers to house sows in conditions where social interactions may lead to competition and conflict, rendering the management of group housing a central welfare and sustainability issue.

However, legislation and societal expectations alone do not guarantee that sows will thrive in group housing. Whilst such systems were introduced to improve animal welfare, they also expose gilts and sows to repeated social challenges, which require careful management. These challenges cannot be addressed by regulation alone; they require a deeper understanding of pigs and how management, breeding and early-life conditions interact to support welfare in practice.

2.1.2 Science and animal welfare assessment

Animal welfare is a multidimensional concept that refers to the animal's physical and mental state in relation to its living conditions and its capacity to cope with environmental challenges (Broom, 1986; Hemsworth *et al.*, 2015; Mellor, 2012). Welfare is understood as a state within the animal, shaped by both biological functioning and affective experiences (Hemsworth *et al.*, 2015). The absence of disease, injury or overt distress does not necessarily imply good welfare as preventing poor welfare is crucial but not sufficient overall for ensuring good welfare (Boissy *et al.*, 2007).

Welfare cannot be measured directly, therefore it is inferred from indicators that reflect different dimensions of the animal's experience (Fraser, 2003; Hemsworth *et al.*, 2015). Behavioural measures provide insight into how animals respond to and engage with their social and physical environment, whereas physical indicators such as skin lesions, lameness and body condition reflect realised exposure to injury, pain or environmental constraints. Resource- and management-based measures further describe the conditions and risks that animals are exposed to.

No single indicator can completely capture welfare. Behaviour alone may not reveal longer-term or cumulative welfare consequences, and physical outcomes do not necessarily explain the behavioural processes that led to them. A comprehensive welfare assessment therefore requires an integration of multiple indicators over time. In the present thesis, welfare is assessed through behavioural observations and outcome-based measures, primarily skin lesions and other health-related indicators, interpreted as outcome-based indicators of potential welfare compromise rather than direct measures of welfare per se. Historically, much of welfare research has focused on reducing negative states, however, increasing attention is now being directed toward understanding conditions that support positive experiences (Lawrence *et al.*, 2019; Rault *et al.*, 2020). Within group-housed systems, this highlights the importance of not only minimising injury and stress, but of also facilitating adaptive social functioning.

2.2 The sow as a social animal

The pig is widely understood to be a social species and this characteristic is particularly evident among sows, whose reproductive success relies on their ability to navigate complex social environments (Jensen, 2022). The social nature of the sow is the result of evolutionary pressures favouring cooperation, group living and the maintenance of stable relationships (Greenwood *et al.*, 2014; Podgórski *et al.*, 2014). Although pigs have been domesticated for thousands of years (Caliebe *et al.*, 2017; Giuffra *et al.*, 2000) and subjected to intense selection for production traits in modern breeding programmes, the essential social nature of pigs remains intact (Collarini *et al.*, 2022; Stolba & Wood-Gush, 1989).

To understand how a pig's social nature interacts with the demands of commercial production, the related production environments and management, it is helpful to first consider the natural context in which the pig evolved, then the effects of domestication and lastly the conditions of modern sow housing systems.

2.2.1 Life in the wild

Ecology and natural behaviour

The wild boar (*Sus scrofa*) is a highly adaptable species native to Europe and Asia that occupies a wide range of habitats, from dense deciduous forests to mixed agricultural landscapes (Podgórski *et al.*, 2013). Their success in these varied environments is largely due to a flexible behavioural repertoire and a broad omnivorous diet (Erdtmann & Keuling, 2020; Podgórski *et al.*, 2013). Wild pigs are opportunistic foragers, consuming various food sources such as roots, green plant material, agricultural crops, invertebrates and small mammals, contingent upon seasonal availability (Schley & Roper, 2003). Foraging and rooting account for much of their active time (Stolba & Wood-Gush, 1989), and their activity patterns are predominantly nocturnal, with pronounced activity peaks at dawn and dusk and resting periods during the warmer parts of the day (Boitani *et al.*, 1994; Keuling *et al.*, 2008). When inactive, wild pigs rest in nests or sheltered areas that provide both insulation and protection from predators (D'Eath & Turner, 2009; Stolba & Wood-Gush, 1984, 1989). These nests, constructed from branches, leaves and soil, are also used for thermoregulation and social cohesion within groups (Jensen, 1986; Stolba & Wood-Gush, 1989).

In natural environments, pigs use space in a structured and predictable manner. Groups maintain a defined home range and repeatedly utilise the same foraging routes, resting sites and travel paths (D'Eath & Turner, 2009; Podgórski *et al.*, 2013). This consistent use of the landscape provides stability and reduces the likelihood of unpredictable encounters with unfamiliar groups (Stolba & Wood-Gush, 1989). If two unfamiliar groups encounter one another, direct confrontation is typically avoided (Gabor *et al.*, 1999). Pigs rely on spatial avoidance and the use of olfactory and vocal cues to decrease the likelihood of conflict with unfamiliar groups that share overlapping home ranges (Marchant-Forde & Marchant-Forde, 2005). When avoidance fails, or when competition over limited resources increases, agonistic interactions may arise between groups (Archer, 1988).

Moreover, in natural environments, pigs live in stable, matrilineal social groups where maternal behaviour forms a central component of the sow's natural ecology (Graves, 1984; Mauget, 1981). Shortly before farrowing, the sow withdraws from her social group and selects a sheltered location for nest construction (Jensen, 1986; Stolba & Wood-Gush, 1989). Using vegetation and soil, she builds a well-structured nest that provides protection and warmth for her offspring (D'Eath & Turner, 2009). The sow remains isolated for several days after parturition, during which she nurses and bonds with her litter without interference from other group members (Jensen, 1986; Stolba & Wood-Gush, 1989). This period of isolation reduces disturbance and aggression towards the newborn piglets and facilitates maternal-offspring bonding. The sow then gradually rejoins the group with her litter, allowing the piglets to adapt to group living early on (Jensen, 1986; Jensen & Redbo, 1987).

Together, access to space and shelter, predictable use of the environment and the opportunity to perform species-specific behaviours such as rooting, resting in nests and nest building before farrowing forms the foundation of the pig's natural behavioural repertoire. These ecological conditions provide stability, reduce unpredictability and support early behavioural development, including the gradual exposure to other group members of varying ages. Under these conditions, the foundations for group living are established, as young pigs learn to coordinate activity, avoid unnecessary conflict and interact within a familiar and stable social environment.

Social organisation

Under natural conditions, wild boars form structured and predictable social groups that play a key role in their behavioural ecology. Female pigs establish stable matrilineal groups that consist of related sows and their offspring, often spanning several generations (Graves, 1984; Podgórski *et al.*, 2014). Group size varies depending on habitat and resource availability (Graves, 1984; Mauget, 1981). They usually consist of two to six adult females and their litters, which forms a highly cohesive unit where females maintain long-term associations and collective responsibilities for offspring survival (Graves, 1984; Kaminski *et al.*, 2005). Larger aggregations may occur in areas with abundant food or during certain seasons, but these are typically more temporary in nature (Dardaillon, 1988).

Within these maternal groups, social relationships develop gradually (D'Eath & Turner, 2009). Hierarchies are established and reinforced through recognition and past experiences rather than frequent aggression (Jensen, 2022). The stability of the group is primarily maintained through avoidance and active submission by the animals that are low in the social hierarchy of the group (Jensen, 2022). This stability reduces the frequency of conflicts and creates a predictable social environment, where pigs interact with familiar group members, recognise established hierarchies and can rely on long-term relationships rather than constantly renegotiating their social position. Cooperation and affiliative behaviours are frequent as sows often rest in close contact, synchronise activity, socially groom and, in some cases, even engage in communal nursing and shared defence of all piglets (D'Eath & Turner, 2009; Fraser *et al*., 1995; Graves, 1984). These behaviours reinforce social bonds and help to maintain unity within the group.

Males follow a different social trajectory. Unlike their female siblings, young boars leave their family group at puberty and may form temporary groups of young males before adopting a more solitary lifestyle (Graves, 1984; Jensen, 2022; Mauget, 1981). The boars typically only join the female groups during the mating periods (D'Eath & Turner, 2009; Jensen, 2022), which further emphasises the maternal group as the core of pig social systems.

The gradual integration of young pigs is another defining feature of pigs' natural group structure. Piglets remain with their mother and the other females and their offspring for several months, enabling opportunities to learn social rules and skills through observation, play and interactions with peers and older individuals (D'Eath & Turner, 2009; Jensen & Redbo, 1987; Petersen *et al*., 1989). Play in particular has been linked to the development of motor and social competence, preparing juveniles for the challenges of adult life (Spinka *et al*., 2001; Weller *et al*., 2019).

These patterns demonstrate that the sow's social competence in adulthood is grounded in lifelong exposure to a structured and predictable social environment. Natural conditions provide a context in which long-term and stable relationships, familiarity and gradual social learning shape individuals that are well equipped for the demands that group living entails.

2.2.2 Domestication

The domestic pig (*Sus scrofa domesticus*) originates from the Eurasian wild boar and was domesticated approximately 7 000–10 000 years ago (Giuffra *et al*., 2000; Larson *et al*., 2005, 2007). Domestication involves both genetic adaptation and developmental processes that occur when animals are managed by humans over many generations (Price, 1984). Although domestication has resulted in considerable changes regarding productivity, morphology and physiology, many fundamental behavioural traits have been largely conserved (Jensen, 2022; Stolba & Wood-Gush, 1989). Studies of domestic pigs kept in semi-natural environments show that they continue to perform the same fundamental behaviours as wild boars, including rooting, foraging, nest building and maintaining social bonds (Gustafsson *et al*., 1999; Jensen, 1986, 2022; Stolba & Wood-Gush, 1984). This suggests that domestication has primarily influenced the expression and frequency of behaviours rather than replacing the behavioural repertoire itself (Price, 1984).

Modern breeding programmes have predominantly targeted production traits such as growth rate, feed efficiency and litter size (Boonkum *et al.*, 2025; Kanis *et al.*, 2005). Behavioural traits have received less attention for systematic change, although some genetic lines differ in aggression, activity or stress responsiveness (Camerlink *et al.*, 2013; Turner *et al.*, 2008, 2009, 2010). Notably, such genetic differences in aggression, activity or stress responsiveness occur within an evolved behavioural repertoire that continues to be shaped by evolutionary pressures for group living and coordinated social behaviour.

Consequently, domestic sows retain behavioural motivations moulded by their ancestral social organisation, even though the environments that they are kept within today differ markedly from natural or semi-natural conditions. Recognising this continuity between wild and domestic behaviour is essential for understanding how sows respond to the social and environmental challenges of modern group housing systems.

2.2.3 Modern sow housing

Traditionally, commercial pig production relied heavily on individual housing systems for both gestating and farrowing sows (Pajor, 2004). From the mid-20th century onwards, the use of tethers, stalls and later farrowing crates became widespread across industrialised production, primarily because these systems simplified feeding, reproductive management and observation of individual pigs whilst reducing physical competition between animals (Barnett *et al.*, 1989; Blackshaw *et al.*, 1994; Robertson *et al.*, 1966). Farrowing crates remain the dominant housing system worldwide during farrowing and lactation, largely due to their perceived advantages for piglet survival and stockperson safety and workload (Baxter *et al.*, 2011; Pedersen, 2018). Today, there is substantial global variation regarding sow housing. In many regions outside the EU, individual gestation stalls continue to be standard practice throughout most or the entire gestation period (Schuck-Paim & Alonso, 2022). These systems enable the precise control of feed allocation and reproductive monitoring, and their continued use reflects production goals, labour resources, infrastructure and welfare regulations. As a result, gilts and sows in these systems often move through a cycle of individually housed facilities during gestation, followed by transfer to farrowing crates during farrowing and lactation.

Within the EU and other regions where welfare standards have encouraged or mandated a shift towards group housing, gilts and sows spend at least part of the gestation period in groups (Baxter *et al.*, 2025). In practice, group housing systems vary widely in size, stability and management (Spoolder *et al.*, 2009). Groups range from small and static, with 8–20 sows per pen, to large and dynamic, with 50–300 animals and frequent changes in group composition (EFSA *et al.*, 2022; Jang & Oh, 2022; Spoolder *et al.*, 2009; Verdon *et al.*, 2015). Feeding strategies also vary between farms; for example, some use floor or trickle feeding, whilst others rely on electronic sow feeding systems that allow for an individualised feed allowance (EFSA *et al.*, 2022; Jang & Oh, 2022; Spoolder *et al.*, 2009; Verdon *et al.*, 2015). Pen layout, flooring, space allowance, resources and the availability of enrichment materials influence how animals distribute themselves and interact within a group housing system (EFSA *et al.*, 2022; Jang & Oh, 2022; Spoolder *et al.*, 2009; Verdon *et al.*, 2015).

In Sweden, group housing plays an even more central role in sow management, as sows are also kept loose throughout both mating and gestation. Farrowing is then carried out in loose-housed pens rather than farrowing crates (SJVFS 2019:20 (L106)). Consequently, the production cycle involves repeated transitions between individual farrowing pens and group housing after weaning, leading Swedish sows to spend a larger proportion of their lives in social groups than sows in most other countries.

Overall, modern sow housing creates social environments that differ substantially from the stable and familiar group structures found in natural pig societies. Variability in group composition, repeated exposure to unfamiliar individuals and movements between housing systems introduce forms of social complexity that are largely absent under natural conditions. These features shape the dynamics of group living in commercial systems and underpin many of the welfare challenges associated with group housing.

2.3 Challenges of housing sows in groups

Whilst group housing allows sows greater freedom of movement and opportunities for social interactions, it also places them in social environments that differ fundamentally from the stable, familiarity-based groups that pig social behaviour evolved from (Arey & Edwards, 1998; Jensen, 2022). Commercial group-housing systems are characterised by repeated mixing of unfamiliar individuals, competition over restricted resources and, in some systems, continuous changes in group composition (Spoolder & Vermeer, 2015). These features introduce periods of social instability and conflict and may amplify individual differences in social competence, coping ability and injury risk (Spoolder & Vermeer, 2015). Importantly, social interactions in group housing can increase both positive and negative interactions. Aggressive behaviour represents the most prominent negative social interaction and this has implications not only for sow welfare and performance but also for the working environment of farm staff (Spoolder & Vermeer, 2015).

A central challenge arises during mixing events, when previously unfamiliar pigs are brought together. Group formation requires the establishment or re-establishment of a dominance hierarchy, a process consistently associated with increased levels of aggression, fighting and competitive interactions (Arey & Edwards, 1998; Greenwood *et al.*, 2014). Aggressive behaviour among sows is typically most intense during the initial hours after mixing and declines thereafter, with dominance hierarchies generally stabilising within 2-10 days (Arey, 1999; Greenwood *et al.*, 2014; Moore *et al.*, 1993; Zurbrigg & Blackwell, 2006). Such behaviour is influenced by factors such as group size, pen design, feeding strategy, the presence of escape opportunities and the level of familiarity among animals (Greenwood *et al.*, 2014; Marchant-Forde, 2009). Although social hierarchies tend to stabilise over time, early conflicts may result in skin lesions and other injuries that can have implications for welfare and production performance (Greenwood *et al.*, 2014; Spoolder & Vermeer, 2015). Most lesions caused by aggression are scratches or cuts on the skin (Spoolder & Vermeer, 2015). Fighting is detrimental to welfare, with the losing animal generally suffering the greatest costs, including for example severe skin damage and locomotion problems (Burfoot *et al.*, 1995; Greenwood *et al.*, 2014; Tönepöhl *et al.*, 2013).

Competition for resources represents another major social challenge within group settings (Greenwood *et al.*, 2014). Aggressive and potentially injurious behaviour is particularly common in relation to feeding. Most commercial systems rely on restricted feeding during mating and gestation, which increases the motivation to access feed and in turn intensifies competition (Barnett *et al.*, 2001; Verdon *et al.*, 2015). In group housing systems for sows, two main types of feeding systems are common: simultaneous and sequential feeding. Simultaneous systems involve animals feeding on one or two occasions per day (Spoolder & Vermeer, 2015). Typical systems for simultaneous feeding are trough feeding with free access stalls, floor feeding and long trough (wet) feeding setups (Spoolder & Vermeer, 2015). In simultaneous feeding systems, the degree of physical protection at the feeding place is crucial. Systems that provide greater separation between animals, for example through longer or fully separating partitions between feeding places, reduce the opportunity for fasteating or dominant sows to displace smaller or slower group mates during feeding (Andersen *et al.*, 1999). Sequential feeding systems involve animals feeding one after another, with electronic sow feeding systems being the most common example (Spoolder & Vermeer, 2015). In sequential feeding systems, it is even more important that the sow is protected in a way so that she cannot be displaced by more dominant sows (Spoolder & Vermeer, 2015). Access to water, lying space, preferred resting areas and brushes can also become resources generating competition, particularly in large or heterogeneous groups (Högberg *et al.*, 2025; Hoy *et al.*, 2009).

Social stability can also be influenced by group composition. Commercial groups typically consist of unrelated sows that vary in parity, size, temperament and social experience. Older, heavier or more dominant sows may monopolise resources, whereas younger or subordinate animals may experience reduced access to feed, water or preferred resting areas (Verdon *et al.*, 2015). Differences in social competence and coping styles could further affect how individuals respond to social pressure, contributing to variation in welfare outcomes within the same housing system (Verdon *et al.*, 2015).

Dynamic group systems, in which animals enter or leave the group at regular intervals, present additional complexity. Each introduction or removal has the potential to disrupt established social relationships, contributing to ongoing instability and repeated periods of increased aggression (Spoolder & Vermeer, 2015). Dynamic group systems generally involve larger group sizes, which presents more opportunities for targeted sows to avoid aggression by blending into the group or moving behind other animals (Anil *et al.*, 2006; Spoolder *et al.*, 2009; Turner & Edwards, 2004). In contrast, static groups remain stable after formation (Verdon *et al.*, 2015), but may offer less flexibility for management. Moreover, environmental factors interact with the social dynamics of the sow group. Pen layout, availability of barriers or escape opportunities, space allowance and enrichment all influence how conflicts unfold and how easily sows can avoid confrontations (Arey & Edwards, 1998; Greenwood *et al.*, 2014; Verdon *et al.*, 2015). Although group housing provides sows with greater freedom of movement and enables social interactions, it inherently involves repeated social challenges that require behavioural flexibility and the ability to cope with social pressure. Poorly designed housing environments may exacerbate the physical consequences of social interactions, meaning that aggressive or competitive encounters not only result in skin lesions but also in locomotor problems arising from slips, falls or excessive physical strain when avoidance is restricted or flooring provides insufficient grip (Spoolder & Vermeer, 2015).

Taken together, group housing creates social environments that differ considerably from natural pig societies, generating both opportunities and challenges for sow welfare and placing a particular emphasis on individual variation in social competence, previous experience and genetic background.

2.4 Sustainability and premature culling

Sow longevity is a key component of sustainable sow production, both from an economic and animal welfare perspective (Moeller & Stalder, 2024). In commercial herds, earlier research has estimated the third parity as the point at which a sow achieves a positive net economic return, meaning she has produced enough offspring to cover her own production costs (Lucia *et al.*, 2000; Stalder *et al.*, 2003; Stalder *et al.*, 2000). Although sows are biologically capable of producing more litters, the reported average parity at removal in Swedish commercial herds in 2023 was 4.0, indicating that the typical sow is culled around her fourth parity (Hidås *et al.*, 2025). This, together with earlier findings, suggests that many sows leave the herd before reaching their full reproductive potential (Engblom *et al.*, 2007; Hidås *et al.*, 2025). Benchmarking data from sow farms in the United States, Canada and Australia indicate that approximately 40–50% of total sow herd mortality occurs before the second parity, highlighting the vulnerability of young breeding gilts and sows (Ketchem *et al.*, 2020). Similarly, data from Swedish piglet producing farms in 2022 indicates that 31% of sows are removed before reaching their third parity litter (Hidås *et al.*, 2025). Early culling reduces lifetime productivity, increases replacement costs and creates challenges for herd stability, making sow longevity an important indicator of economic efficiency. At the same time, when premature removal results from injury, disease or compromised function, it reflects underlying welfare challenges within the production system (Hidås *et al.*, 2025; Moeller & Stalder, 2024).

Premature removal from the breeding herd is not a uniform outcome but encompasses several distinct pathways. Sows may be removed because of planned culling decisions, involuntary culling due to health or welfare problems (typically resulting in slaughter) or mortality, including both spontaneous death and on-farm euthanasia (Moeller & Stalder, 2024). Whilst these categories differ in cause and management implications they share the same consequences of shortening the sow’s productive lifespan and reducing herd sustainability.

Reasons for culling and removal of sows are multifactorial and vary between herds, but common causes include reproductive failure, udder problems, lameness, injury and inadequate performance (Engblom *et al.*, 2007; Hidås *et al.*, 2025). Social stress and injuries arising from repeated mixing and competition may contribute to several of these outcomes, particularly when animals struggle to adapt to dynamic or competitive social environments (Greenwood *et al.*, 2014; Spoolder *et al.*, 2009). Gilts and younger sows may be particularly vulnerable, as they must simultaneously cope with new social environments, develop maternal competence and sustain productivity across the first reproductive cycle (Greenwood *et al.*, 2014; Hoy *et al.*, 2009). Consequently, the early reproductive period, parities 0 to 2, often represents a critical window for both survival in the herd and future performance.

Evidence from large-scale Nordic studies underscores that premature removal is not an isolated phenomenon, but a general sustainability challenge in modern sow production systems. National data from Denmark consistently demonstrates high in-herd sow mortality, including both spontaneous deaths and on-farm euthanasia. Notably, average annual mortality rates were approximately 10% during 2015-2018, which increased to around 14–15% in conventional herds by 2021-2022, alongside substantial variation between herds (Kongsted & Krogh, 2025). These findings indicate that losing sows before the end of their expected productive lifespan is widespread and structurally embedded at the system level. Although housing design and management practices differ between Denmark and Sweden, both countries require group housing for gestating sows during most of the gestation period. However, Danish regulations include transitional provisions allowing individual housing during early gestation in some systems until 2035 (BEK nr 15, 2026, §§65, 88–89), meaning that comparisons should be made cautiously when interpreting system-level patterns of premature removal. Swedish farm-level data from 2022–2023 shows that unplanned culling constitutes a considerable proportion of removals, with approximately 16 % of sows removed from production not being sent to slaughter (Wallenbeck *et al.*, 2024). Importantly, most unplanned removals occur during the group housing period between weaning and farrowing, and early parity sows (parity 1–2) face a significantly higher risk of involuntary removal than older sows, which are more frequently removed through planned slaughter (Wallenbeck *et al.*, 2024).

Variation in sow longevity therefore reflects differences in management and housing, but also in individual behavioural strategies and differences in health and functional capacity. Sows that cope poorly with social pressure, competition or environmental constraints may experience decreased feed intake, more injuries or poorer reproductive outcomes, increasing the likelihood of premature removal (Spoolder & Vermeer, 2015). Conversely, individuals that exhibit social competence, such as effective avoidance patterns, stable participation in group interactions or efficient use of resources, may be better suited to functioning within group-housed systems (Van Putten & Buré, 1997).

Premature removal therefore signals underlying welfare challenges at the individual level and represents a broader sustainability concern, as early removal increases replacement needs, resource use and herd turnover. From this perspective, sow longevity is not a separate concept but rather the long-term expression of premature removal patterns, which reflects how well the production system supports sows to remain healthy, cope with challenges and function over time.

2.5 Gilt early life social environments

Early-life social environments have been studied as potential determinants of behavioural development and social competence in pigs. Mixing of unfamiliar piglets after weaning is well known to trigger intense aggression and competition as dominance relationships are established (Friend *et al.*, 1983; McGlone, 1985; Rundgren & Löfquist, 1989). As this is a predictable pattern, numerous studies have investigated whether increasing social contact before weaning can reduce aggression and promote more adaptive responses during subsequent regrouping (Camerlink *et al.*, 2018; D'Eath, 2005; Fels *et al.*, 2021; Hessel *et al.*, 2006; Morgan *et al.*, 2014; Salazar *et al.*, 2018; Wattanakul *et al.*, 1997; Weller *et al.*, 2019, 2020).

Early social experience before weaning, achieved through various forms of social contact between litters, has been shown to shape later social behaviour and has been discussed as a way to increase young pigs' social skills (D'Eath, 2005; Wattanakul *et al.*, 1997). Socialised piglets tend to partake in fighting for shorter durations due to being more decisive in aggressive interactions and hence forming dominance relationships faster (D'Eath, 2005; Hessel *et al.*, 2006). Early socialisation has been associated with reduced consequences of aggression, such as fewer skin lesions (D'Eath, 2005; Hessel *et al.*, 2006; Kanaan *et al.*, 2012; Salazar *et al.*, 2018). The effects from early social experience are often interpreted as evidence that early social contact accelerates the development of social skills, including recognition, assessment and avoidance strategies.

However, results are not fully consistent across the literature. When early social contact is implemented in farrowing crates or very small pens, piglets may have limited opportunities to practise avoidance, assessment or non-agonistic interactions, reducing the potential for detectable benefits at post-weaning regrouping (Van Kerschaver *et al.*, 2023). Other studies have reported that any early benefits disappear once pigs are placed in highly competitive environments, such as restricted feeding, low space allowance or large unfamiliar groups, where resource pressure outweighs prior social experience. In some cases, early socialised piglets do not differ from controls in lesion scores, aggression levels or growth performance after regrouping (Ko *et al.*, 2020; Kutzer *et al.*, 2009; Morgan *et al.*, 2014; Verdon *et al.*, 2020).

The generalisability of existing findings is also limited by the populations and systems studied. As illustrated by the overview provided by Van Kerschaver *et al.* (2023), most studies on pre-weaning socialisation have been conducted on pigs reared for slaughter, with follow-up typically restricted to the pre- or post-weaning period. Pigs held for slaughter are usually reared in other housing conditions, with a different regrouping frequency and behavioural demands from those experienced by breeding females. As most studies have focused on slaughter pigs and short-term outcomes, evidence on the long-term effects of early social experience in replacement gilts remains limited. Furthermore, many early studies were performed in systems dominated by farrowing crates, or in experimental setups with non-commercial space allowances, which further complicates extrapolation to loose-housed sow systems.

Environmental conditions also contribute to behavioural development, although the effects vary across studies. Access to manipulable materials has been shown to increase exploratory behaviour and minimise the risk of redirected or damaging behaviours (Wen *et al.*, 2021). Again, the persistence of these effects strongly depends on the environment encountered after weaning.

Taken together, the existing literature demonstrates that both early-life socialisation and environmental conditions can shape behavioural development in pigs, but the strength, direction and longevity of these effects depend on housing design, space allowance, feeding regime, group composition and the social demands imposed later in life. Whilst the evidence from pre-weaning socialisation studies is valuable, much remains unknown about how early experiences translate into long-term social competence in breeding gilts.

2.6 Genetic background and behavioural differences

Genetic variation contributes to individual differences in behaviour, stress responsiveness and social behaviour in pigs. Heritable genetic variation among pigs can be seen in traits such as aggression (Løvendahl *et al.*, 2005; Turner *et al.*, 2010), fearfulness and exploratory tendencies (Desire et al., 2023), as well as broader temperament patterns often described as coping styles (Bergsma *et al.*, 2008). These behavioural traits could be linked to how animals assess unfamiliar conspecifics, establish dominance relationships and adapt to social challenges, i.e. linked to processes central to the functioning of pigs in group-housed production systems.

Commercial breeding programmes have traditionally focused on productivity traits, such as growth rate, feed efficiency, carcass composition and reproductive performance (Turner *et al.*, 2024; Vaishnav *et al.*, 2025). In some cases, breeding programmes have also included functional traits such as health-related traits but then with a much smaller emphasis on the selection than that of production traits (Turner *et al.*, 2024; Vaishnav *et al.*, 2025). Although production focused breeding goals continue to dominate there can be unintended welfare consequences. Selection for production traits can lead to correlated genetic change in other traits through pleiotropy or linkage, including traits related to damaging social behaviour (Turner *et al.*, 2024). Such indirect effects are often explained by unfavourable genetic correlations between production traits and behavioural or welfare-related traits, as opposed to intentional selection against traits that are important for animal welfare (Turner *et al.*, 2024).

Moreover, to favour sow performance in group-housed systems in breeding, it is important to include knowledge about genotype-environment interactions, where traits (production and/or behavioural) may be expressed differently under varying levels of social demand (e.g. individual stalls or group housing).

This raises the question of whether behavioural patterns that are shaped indirectly through productivity-focused selection align with the demands of contemporary systems, where repeated regrouping and sustained social interactions place considerable behavioural demands on gilts and sows. Whilst indirect genetic effects, where an individual's behaviour influences the welfare or performance of its group mates, have been proposed as potentially important (Camerlink *et al.*, 2013), research specifically addressing social genetic effects in group-housed commercial sows remains limited.

However, previous studies demonstrate that social behaviour in pigs possesses a heritable component (e.g. Løvendahl *et al.*, 2005; Turner, 2011;

Turner *et al.*, 2009, 2010). At the same time, its expression is strongly influenced by social context and group composition (Turner *et al.*, 2010). For aggressive interactions in particular, phenotypic outcomes reflect both environmental factors, such as housing design and management, and the genetic contributions of multiple individuals. This reflects both direct genetic effects on an individual's own behaviour and associative genetic effects which arise from the other pigs in the group (Turner, 2011). Consequently, genetic contributions to social behaviour may not manifest as consistent or easily detectable differences between lines or breeds, but rather as variation expressed differently depending on housing conditions, group structure and management practices. This complexity complicates direct comparisons across studies and limits the generalisability of reported line differences.

Overall, the existing evidence indicates that genetic background contributes to variation in behavioural patterns, competitiveness and stress responsiveness in pigs, but it remains unclear to what extent these differences influence long-term welfare, injury risk or retention in sows in commercial production. Recognising that breeding goals have historically emphasised productivity over social functioning provides a rationale for examining behavioural responses in animals developed under contrasting historical selection and housing environments.

2.6.1 Swedish Yorkshire and Dutch Yorkshire lines

The two genetic lines included in this thesis, Swedish Yorkshire (SY) and Dutch Yorkshire (DY), offer an opportunity to examine how differences in housing and management conditions that the lines are genetically evaluated and selected in may be reflected in behavioural responses under standardised test conditions.

SY has long formed part of the Swedish maternal line structure together with Swedish Landrace (Lundeheim, 2017) which has been maintained for several decades within a national production system characterised by legislation that requires loose housing for all pigs and group housing during mating and gestation (SJVFS 2019:20, (L106)); (Lundeheim, 2017). In Sweden, sows and gilts are group-housed throughout gestation, with only a brief period of individual housing around farrowing. Following weaning, sows are regrouped and remain in groups during the subsequent gestation cycle, whilst gilts are continuously group-housed until their first farrowing. The genetic selection of SY has therefore been based on evaluating animals in groups and in loose-housed systems since the late 1980s. Thus, Swedish maternal lines have historically developed under conditions of sustained social exposure across the reproductive cycle and potential genetic change in favour of this production environment has accumulated over many generations.

DY, by contrast, was introduced into Swedish production in the early 2010s due to its favourable productivity and large litter size (Lundeheim, 2017). DY originates from Dutch breeding programmes that selected based on performance under a different regulatory and management context. In the Netherlands, group housing of pregnant sows became a legal requirement in 2013, in accordance with the implementation of EU legislation (Dir 2008/120/EC), which requires sows to be housed in groups from four days after insemination until one week before farrowing (Besluit houders van dieren, 2026). Prior to this regulatory change, sows were typically housed individually for the whole gestation period, and selection within Dutch breeding programmes therefore largely occurred under conditions characterised by limited and discontinuous social contact.

A fundamental principle in animal breeding is that evaluation and selection should take place in the environment in which the animals and their offspring are expected to perform and reproduce. Behavioural tendencies shaped under one housing and management context may therefore persist even after the population is introduced into new production systems, particularly when only a limited number of generations have been evaluated under the new conditions. Consequently, historical differences in housing, social exposure and management may continue to influence behavioural responses, even in the absence of intentional selection for behaviour. These background contrasts do not imply deterministic genetic effects. Rather, they provide a biologically and breeding-relevant rationale for examining whether animals that have developed under different historical selection environments respond differently to the social demands of modern group housing.

2.7 Theoretical perspectives for understanding individual variation in behavioural responses to social challenges in group-housed sows

Understanding individual variation in how gilts and sows cope with group housing requires concepts that capture both individual capacity and how well the individual is suited to the demands of the surrounding social environment. In this thesis, concepts such as resilience, social competence, coping strategies and genotype-environment interactions are used as interpretative perspectives rather than deterministic explanations. Together, they provide lenses through which behavioural responses to repeated regrouping, competition and social instability in modern sow production can be understood.

2.7.1 Resilience in group-housed sows

Resilience refers to an individual's capacity to respond to challenges with minimal disruption or to efficiently regain a pre-challenge state, reflecting lower sensitivity or greater adaptive capacity rather than the absence of stress (Colditz & Hine, 2016). In group-housed sows, resilience could be discussed in relation to repeated regrouping events, competition for feed, resting areas or other resources, and the variable and sometimes unpredictable nature of commercial gestation systems. However, evidence regarding resilience in group-housed sows remains limited, and much of the available research has focused on young pigs or controlled experimental settings rather than mature breeding females under commercial conditions (Liu *et al.*, 2021; Luttman *et al.*, 2023; Steinerova, 2025). Resilience likely reflects both developmental influences and inherited behavioural patterns, but how these factors interact under real production conditions is not yet well understood. As sows experience repeated social challenges across multiple reproductive cycles, variation in resilience, i.e. variation in reaction norms, may contribute to differences in injury risk, stress sensitivity and long-term retention in the herd. Thus, resilience serves as a useful conceptual lens for interpreting behavioural variation.

2.7.2 Social competence and coping strategies

Social competence refers to an individual's ability to flexibly adjust its social behaviour to meet the demands of the social environment (Varela *et al.*, 2020). For pigs, this may involve assessing opponents, recognising familiar and unfamiliar individuals, avoiding unnecessary escalation and altering behaviour according to the specific social situation.

In this thesis, a distinction is made between social skills and social competence. Social skills refer to specific behavioural capacities, such as recognition, assessment, signalling or avoidance. Social competence, in contrast, refers to the broader ability to use these behaviours flexibly and appropriately across different social situations. Thus, social skills can be seen as elements of social competence, whereas social competence reflects how effectively these behaviours are adjusted and expressed within a given social situation.

Coping styles describe consistent ways in which individuals respond to challenges (Reimert *et al.*, 2014). They are typically defined as correlated behavioural and physiological stress responses that are consistent over time (Kanitz *et al*., 2019). Coping styles are often discussed in terms of proactive and reactive tendencies (Kanitz *et al*., 2019). Proactive animals tend to display aggression, routine formation and lower behavioural flexibility, whereas reactive animals rely more on avoidance, caution and context-dependent behaviour (Janczak *et al*., 2003). Neither style is universally advantageous; effectiveness depends on the demands of the environment. In the present thesis, physiological stress markers were not assessed.

In large, dynamic groups, where social conditions change frequently, behavioural flexibility may be especially important. Behavioural flexibility describes the extent to which an individual modifies their behaviour in response to changing environmental and social cues (Coppens *et al*., 2010). Individuals differ in how strongly their behaviour is guided by external stimuli versus more rigid, internally driven patterns, and this flexibility is often considered a relatively stable characteristic associated with coping style (Coppens *et al*., 2010). In group-housed systems, behavioural flexibility may be particularly relevant during situations that require rapid social assessment and adjustment, such as mixing, competition for resources and changes in group composition.

Most studies on coping and social competence are based on controlled behavioural tests or young pigs, therefore their significance for mature breeding females is uncertain. Nevertheless, these concepts offer a valuable framework for interpreting why individuals differ in their responses to social challenges in commercial group-housing systems.

2.7.3 Genotype by environment interactions

Genotype by environment interactions offer a valuable perspective for interpreting potential line differences observed in this thesis. Rather than assuming that behavioural differences between genetic lines are consistently expressed across conditions, this perspective emphasises that such differences may only become apparent under specific social and management conditions. Genetic lines that have developed under contrasting historical housing and management conditions may therefore differ in how behaviours are expressed when animals are exposed to the repeated social challenges characteristic of modern group-housed production systems.

3. Aims

The overall aim of this thesis is to contribute to knowledge about individual variation in behaviour and welfare in group-housed gilts and sows that is relevant for the development of commercial pig production. The work focuses on early-life social experiences, genetic background and responses to social challenges, as well as welfare indicators related to group housing of sows in commercial herds.

More specifically, this thesis has the following objectives:

- ➢ to investigate whether early social experiences and genetic line are associated with behavioural patterns, social responsiveness and behaviour-lesion relationships to social challenges across various life stages of gilts and sows (Study I - Papers I-IV).

- ➢ to describe the prevalence, location and severity of skin lesions, lameness and body soiling in group-housed sows and gilts on commercial Swedish farms, and to explore potential associations with housing and management factors (Study II -Paper V).

3.1 Overarching research questions

Based on the aims above, this thesis addressed the following overarching research questions:

- How do early-life social environment and genetic background relate to behavioural development and social responses across life stages in gilts and sows?
- How are behavioural patterns during social challenges associated with lesion outcomes, and how are these associations related to early-life social experience and genetic background?
- How are welfare-related indicators, including lesions, lameness and body soiling, distributed in Swedish commercial group-housing systems, and how do management-related factors relate to their occurrence?

4. Material and methods

This thesis comprises two main studies. Study I (Papers I–IV) involved a series of experimental and semi-experimental studies conducted under controlled conditions at SLUs research herd, focusing on behavioural development, social interactions and responses to social challenges in gilts and sows at different life stages. Study II (Paper V) was performed as an observational cross-sectional study on commercial Swedish pig farms and addressed the prevalence and distribution of welfare indicators in group-housed gilts and sows. Detailed descriptions of experimental procedures, data collection and statistical analyses are provided in the published papers (Papers I-IV) and manuscript (Paper V) which are included at the end of the thesis.

4.1 Ethical statement

All experimental procedures included in Study I (Papers I–IV) were approved by the National Ethics Committee for Animal Experiments in Uppsala (registration number 5.8.18-16279/2017) and conducted in accordance with Swedish animal welfare legislation (Swedish Animal Welfare Ordinance, [2019:66]). The studies were carried out under controlled conditions, and animals were handled by trained personnel. Behavioural observations were non-invasive, and social challenge tests were performed with close monitoring of the animals to minimise stress and the risk of injuries.

Study II (Paper V) was based on welfare assessments conducted during on-farm visits to commercial pig farms. The study did not involve any experimental procedures, interventions or deviations from routine animal housing and management. Thus, ethical approval was not required according to Swedish national legislation (7 chap. 7§ Animal welfare ordinance [2019:66]).

4.2 Study I (Papers I – IV)

Study I comprised a series of interrelated experimental and semi-experimental studies conducted as part of the larger research project. The studies were carried out at the pig facility at the Swedish Livestock Research Centre of the Swedish University of Agricultural Sciences (Lövsta) between 2018 and 2020. In total, 98 gilts were followed from early life through gilt rearing and into their first parity.

The gilts were born as either 100 % Swedish Yorkshire (SY) or at least 75 % Dutch Yorkshire (DY). For the SY gilts, frozen semen was used for insemination. This was collected prior to the change in housing-policy of sows in the EU in 2013 (Dir 2008/120/EC) which also affected sow housing in the Netherlands. These gilts were subjected to different early social environments during the suckling period. To create an early environment with additional social mixing, litters were housed with individually loose-housed sows either in systems allowing social contact between neighbouring litters (Access pens, AP) or conventional farrowing pens without openings between neighbouring pens (Closed pens, CP), which commenced at approximately two weeks of age. After weaning at 5 weeks of age (marking the end of the early social mixing environment period), gilts were housed with littermates, i.e. no unfamiliar individuals, until approximately 10 weeks of age. The gilts were then moved to a gilt-rearing stable in groups of four. To create a late social mixing environment, they were either placed in an intact group (IG), where they were housed with gilts from their own farrowing litter, or mixed groups (MG), which consisted of gilts from two birth litters, meaning that each gilt was mixed with one familiar and two unfamiliar gilts. As the gilts reached 20 weeks of age, they were moved to the sow barn and kept in their previously established groups of four (no further mixing occurred) until later insemination and gestation, before being individually moved to farrowing pens in the farrowing units the week before their first farrowing. After weaning of their first litter, primiparous sows were introduced into loose-housed sow groups according to standard production routines, thereby entering a new social environment involving unfamiliar conspecifics.

Due to practical constraints related to housing capacity and management routines at the Lövsta research facility, animals were enrolled in the study in successive batches. In total, seven batches were included over the study period, with gilts progressing through the same production system but at different time points.

The same gilts were followed and assessed across all experimental components of Study I, from early life through gilt rearing and into the first parity. The number of animals included in the individual analyses differed between papers depending on study-specific inclusion criteria and data availability. An overview of the distribution of gilts across papers, genetic lines, and early and late social mixing environments is presented in Figure 1. The study design and experimental timeline for Study I are illustrated in Figure 2.

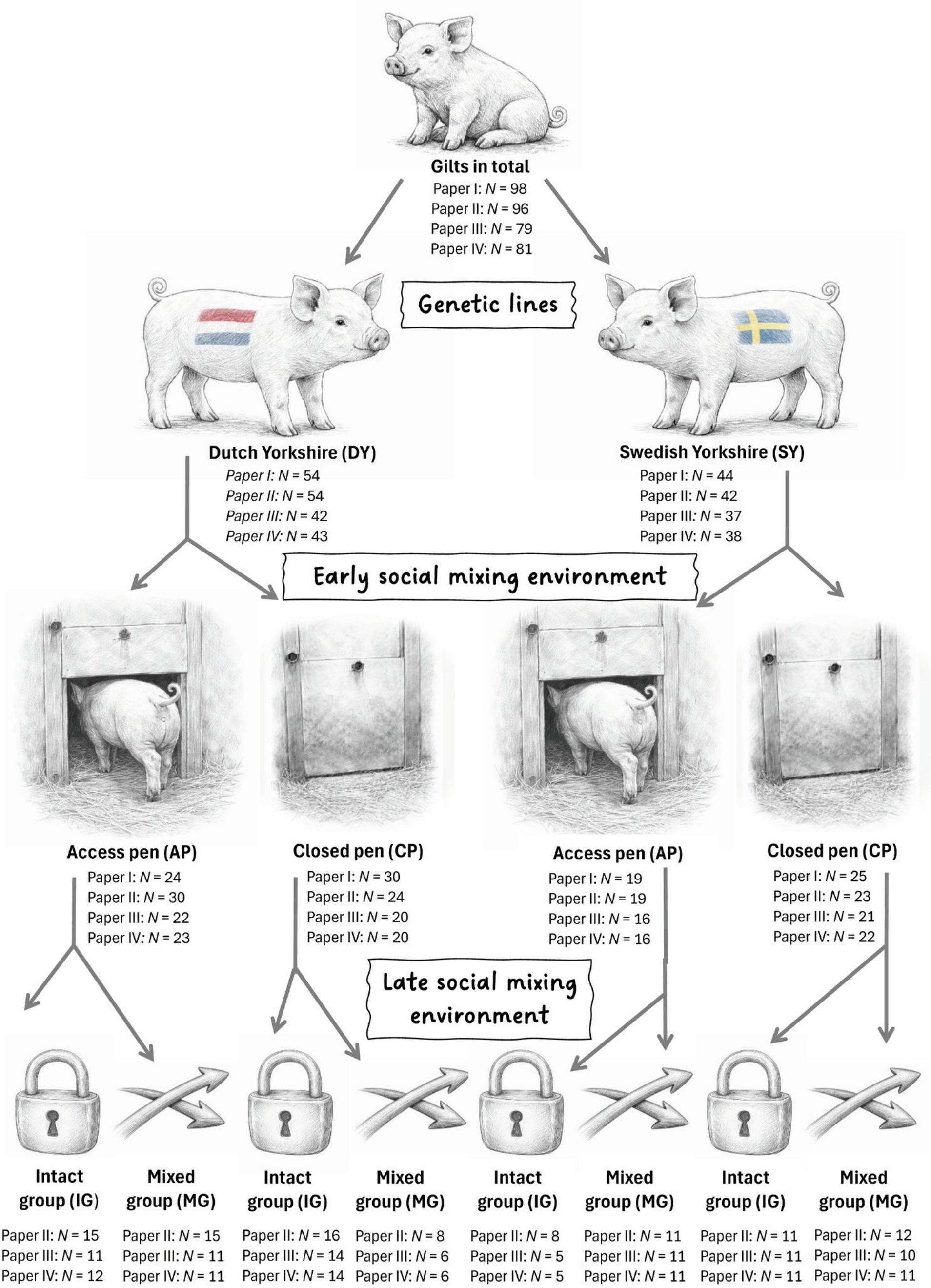


Figure 1. Overview of the experimental design and sample sizes across studies. Female pigs (gilts) from two genetic lines, Dutch Yorkshire (DY) and Swedish Yorkshire (SY), were reared under different early social mixing environments (access pens, AP, or closed pens, CP) and later exposed to different mixing environments (intact groups, IG, or mixed groups, MG). Numbers indicate the sample size included in each paper (Papers I–IV) at each stage of the experimental design.

4.2.1 Paper I - Early social mixing environment and behavioural development

Paper I examined the effects of early social mixing environment and genetic line on behavioural development in gilts before and after weaning. The paper focused on behavioural expression during early life, with particular emphasises on activity, social interactions and use of space within the pen.

This paper included 98 gilts from SY and DY lines, reared in AP or CP systems, where AP allowed pre-weaning mixing with a neighbouring litter. An overview of the distribution of animals across genetic lines and early social environments is presented in Figure 1. Direct observations of body posture, location in pen and social behaviours were performed on eight specific occasions during the first 10 weeks of the gilts' lives (Figure 2).

Recorded behaviours included body posture, analysed as time spent lying (with reduced lying interpreted as higher activity), location within the pen (percentage of scans spent in the piglet corner) and a range of social interactions recorded during direct observations. For AP gilts, posture and pen location in weeks 3-4 were recorded separately for the home pen vs the neighbouring pen. Social interactions included several behaviours relevant for young piglets (e.g. nosing, belly nosing, pushing and biting different body parts), as well as the receiving pig's response to social interactions (avoiding, return approach or no reaction).

The observation schedule was structured to capture behavioural responses associated with key developmental and management-related events during early life, including the period before and after the pop-hole was opened, the period of early social mixing, and the period following pop-hole closure and weaning. This allowed behavioural development to be assessed longitudinally within individuals across distinct social and environmental conditions.

The experimental design of Paper I enabled comparisons between early social mixing environments and genetic lines, as well as within-individual comparisons over time. Detailed descriptions of the behavioural observation protocol and statistical analyses are provided in Paper I.

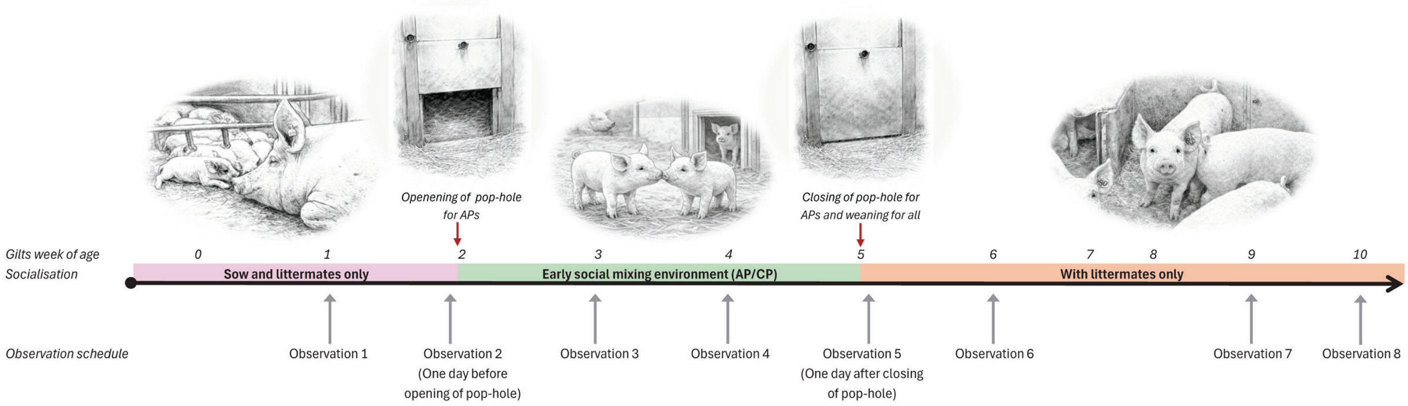


Figure 2. Timeline of gilt age, socialisation phases and observation schedule in Paper I. From birth until 2 weeks of age, gilts were housed with the sow and littermates only. Between weeks 2 and 5, gilts were reared under either an early social mixing environment (access pens, AP) or a closed pen environment (CP), with the pop-hole opened for AP gilts at week 2 and closed at weaning (week 5). After weaning, gilts were housed with littermates only. Arrows indicate the timing of behavioural observations, including observations conducted one day before opening and one day after closing the pop-hole.

Data handling and statistical analyses

Data editing, descriptive statistics and statistical analyses for Paper I were performed using SAS version 9.4 (SAS Institute Inc., 2013). Behavioural data were analysed using mixed-effects models to account for repeated observations of individuals across observation weeks.

Behavioural variables recorded using scan sampling (e.g. body posture and pen location) were analysed using linear mixed models (PROC MIXED), with the percentage of scans per piglet and observation week as the response variables (lying; piglet corner). Social behaviours recorded using continuous sampling were converted to binomial variables per piglet and observation week and analysed using generalised linear mixed models with a binomial distribution and logit link (PROC GLIMMIX), where the response variable indicated whether each behaviour occurred during the continuous observation period that week (yes/no).

The models included early social mixing environment, genetic line and observation week as fixed effects. Interactions between early social mixing environment and observation week, and between genetic line and observation week, were included to assess changes in behavioural expression over time. Batch was included as a fixed effect to account for animals being included in the study in seven successive batches over time. Individual gilt was included as a repeated random effect to account for repeated measurements within individuals across observation weeks. The interaction between genetic line and early social mixing environment was tested but not retained in the final model.

Model assumptions for continuous outcomes were evaluated using residual diagnostics (PROC UNIVARIATE). Results are presented as least squares means with standard errors for continuous outcomes and as estimated probabilities for binomial outcomes. Statistical significance was set at $P < 0.05$. Further details of the statistical analyses are provided in Paper I.

4.2.2 Paper II – Behavioural responses of young gilts in paired interaction tests

Paper II investigated behavioural responses of gilts during a standardised social challenge using a three-minute paired interaction test performed at 5 and 20 weeks of age. The aim was to assess individual behavioural strategies and social responsiveness during an encounter with an unfamiliar conspecific.

This paper was based on 96 gilts from the overall Study I cohort and thus included gilts with different genetic lines (SY/DY) and early social mixing environments (AP/CP). Prior to testing at 20 weeks of age, the same individuals had been subjected to different late social mixing environments, meaning they were housed either in intact groups (IG) or mixed groups (MG), which were initiated at approximately 10 weeks of age. An overview of the distribution of gilts across genetic lines and social environments in this paper is provided in Figure 1.

Paired interaction tests were conducted at two developmental stages, 5 and 20 weeks of age. The test at 5 weeks of age captured behavioural responses at the time of weaning, whereas the test at 20 weeks assessed behavioural responses following prolonged exposure to the late social mixing environment. During the test at 5 weeks of age, each focal gilt was paired with an unfamiliar opponent gilt from the same batch that was not part of the focal study cohort and was weight-matched to the focal gilt. During the test at 20 weeks of age, each focal gilt was paired with another focal gilt from the study, who was always from the other early social mixing treatment. The test duration was three minutes, and behaviour was recorded continuously from video recordings. As both gilts in the 20-week test were focal animals, video recordings were analysed twice, once per focal individual. Examples of the paired interaction test arenas used at 5 and 20 weeks of age are presented in Figures 3 and 4.

Figure 3. Example of the paired interaction test (PIT) arena used at 5 weeks of age. The test was conducted in a neutral area within the same farrowing unit in which the gilts were housed. Each gilt was paired with an unfamiliar opponent in a 3-minute test. The arena consisted of a concrete floor with tread plates on either side, bounded by pen walls and movable gates.

Figure 4. Example of the paired interaction test (PIT) arena used at 20 weeks of age. The test was conducted in a corridor outside the stable, physically separated from the housing pens. Each gilt was paired with an unfamiliar opponent from the study in a 3-minute test. The arena consisted of a concrete floor partially covered with metal tread plates and was bounded by movable gates.

Behavioural measures included latency to first contact, spatial proximity between the two pigs, exploratory behaviour directed towards the test arena and social interactions between the focal gilt and the opponent. Social interactions were recorded separately for behaviours performed by the focal gilt and for the focal gilt's responses to social interactions.

The experimental design enabled within-individual comparisons of behavioural responses across developmental stages, as well as comparisons between individuals subjected to different early and late social mixing environments and genetic backgrounds, as defined in the overall study design. Detailed descriptions of the paired interaction test procedure, test arenas and behavioural recordings are provided in Paper II.

Data handling and statistical analyses

Behavioural data were extracted from BORIS (Friard & Gamba, 2016) and compiled in Microsoft Excel prior to statistical analyses. Due to technical limitations with a video recording, sample sizes differed slightly between test occasions: the paired interaction test conducted at 5 weeks of age included 95 gilts, whilst the test at 20 weeks of age included 94 gilts. All statistical analyses were performed in R (R Core Team, 2024), using functions in the base stats package and associated packages for model inference. The level of statistical significance was set at $P < 0.05$.

Data from the paired interaction tests performed at 5 and 20 weeks of age were analysed separately due to differences in developmental stage. Model development followed a backward stepwise approach, where initial models included biologically relevant main effects and interactions, and non-significant terms were removed based on statistical support, model fit and biological relevance. Where possible, harmonised model structures were applied across response variables with similar distributions.

Latency to first contact was analysed as a continuous variable using Gaussian generalised linear models (GLMs). Binary outcomes related to the initiation of social contact, including whether the focal gilt approached first and whether the first interaction occurred on the focal gilt's starting side of the arena, were analysed using binomial generalised linear models with a logit link function.

Behaviour recorded during the test was analysed at the level of observation minute per focal gilt. Spatial proximity between the two pigs, expressed as the proportion of scan samples spent in close contact, was analysed using Gaussian models. Binary behavioural outcomes per minute, including play behaviour, performance of social interactions and response to social interactions, were analysed using binomial models. Exploratory behaviours directed towards the test arena, recorded as counts per minute, were analysed using Poisson models.

For the paired interaction test conducted at 5 weeks of age, fixed effects included genetic line and early social mixing environment of the focal gilt, as well as observation minute where applicable. For the test conducted at 20 weeks of age, fixed effects included genetic line, early social mixing environment and late social mixing environment of the focal gilt, as well as observation minute. In addition, opponent characteristics were included as fixed effects in models for the 20-week test, specifically opponent genetic line and opponent late social mixing environment. Opponent's early social mixing environment was not included, as focal gilts at 20 weeks of age were consistently paired with opponents from the other early social mixing treatment.

Overall effects and interaction structures were evaluated using joint tests of model terms. When significant effects were detected, post hoc pairwise comparisons were performed using estimated marginal means, with Bonferroni adjustment applied to control for multiple comparisons. Complete descriptions of the statistical models and analytical procedures can be found in Paper II.

4.2.3 Paper III – Behavioural responses and lesion development in primiparous sows during paired interaction tests

Paper III examined behavioural interactions and short-term welfare indicators in primiparous sows, i.e. the same individuals followed from gilt rearing in Study I, exposed to an unfamiliar older conspecific during a standardised social challenge after weaning of the first litter. The study focused on social behaviour, response behaviours and skin lesion development during a production stage that is associated with a high risk of aggressive interactions.

This paper included 79 primiparous sows from the longitudinal Study I cohort and was comprised of animals from two genetic lines (SY/DY) that had been subjected to different early (AP/CP) and late (IG/MG) social environments during rearing. An overview of the distribution of animals across genetic lines and social environments is provided in Figure 1.

Following weaning of their first litter, each primiparous sow was subjected to a paired interaction test (PIT) with an unfamiliar older multiparous sow. The test was conducted in the pen where the young sow would subsequently be housed, thereby reflecting a biologically and management-relevant social challenge under standardised conditions. Each test lasted 60 minutes; however, behavioural analyses focused on the initial 20 minutes during which most social interactions occurred, and the final 10 minutes of the test period, to assess behaviours performed after the initial interaction phase. An example of the PIT set-up used for primiparous sows paired with an unfamiliar older sow is presented in Figure 5.

Figure 5. Example of the paired interaction test (PIT) arena used after weaning of the primiparous sow's first litter. The test was conducted in the pen that was later used for group housing, with a deep straw bedding and standard commercial pen fittings. Feeding stalls closest to the camera were locked to prevent access during the test.

A total of 47 unique older multiparous sows were used as test partners across the 79 PITs, meaning that some older sows were used in more than one test. Of these older sows, 25 were used once, 12 twice, 6 three times and 2 four times, typically across different parities. In three PITs (in total involving two older opponent sows), the test partner had previously participated in the PIT as a first parity sow (FPS). The older sows were relatively homogeneous (mean ± SD), with a parity of 6.06 ± 1.55 and a body weight of 262.9 ± 28.5 kg and were predominantly of the DY line (91.5%).

Parity and body weight did not differ significantly between gilt genetic lines (SY/DY) or social mixing environments (AP/CP and IG/MG) (all $p > 0.15$).

Behaviours performed during the PIT were recorded using video observations and later analysed according to a detailed ethogram. Both behaviours performed by the initiating sow and behavioural responses displayed by the receiving sow were recorded, allowing social exchanges to be characterised across affiliative, warning and damaging interactions, as well as the responses elicited by these behaviours. In addition, the body region targeted during physical interactions was recorded.

Skin lesions and lameness were assessed on the primiparous sows immediately before and after the PIT using a standardised welfare assessment protocol. Lesions were recorded by body region and severity, enabling both total lesion scores and region-specific lesion patterns to be analysed in relation to observed behaviour.

This experimental design allowed for an investigation of associations between social behaviour, response strategies and short-term welfare outcomes during a critical social transition in early sow life. Further methodological details are provided in Paper III.

Data handling and statistical analyses

Behavioural data were extracted from video recordings using BORIS (Friard & Gamba, 2016). Lesions were assessed on-site immediately before and after the test, prior to statistical analyses. All statistical analyses were performed in R (R Core Team, 2024), and statistical significance was set at $P < 0.05$.

Behavioural data from the PITs were analysed according to behavioural category and data structure. Social behaviours and response behaviours were classified based on a predefined ethogram and analysed as counts of events or responses.

Given the count-based nature of most behavioural outcomes and the presence of overdispersion, generalised linear mixed modelling approaches were applied, primarily using negative binomial distributions fitted in glmmTMB. Fixed effects included genetic line, early and late social mixing environments, as well as relevant behavioural predictors. Interaction terms were evaluated and retained when supported by model fit and biological interpretability. Random effects and alternative model structures were explored during model development.

Skin lesion scores were analysed both as total counts and by body region using similar modelling approaches for count data. Zero-inflated model structures were evaluated and retained when clearly supported by an improved model fit.

For analyses focusing on response behaviours, models evaluated whether the frequency of specific responses depended on the type of behaviour received from the unfamiliar sow, and whether these associations differed between genetic lines or social environments.

Model fit and assumptions were assessed using residual diagnostics and comparisons of alternative model structures based on information criteria. When significant effects were detected, estimated marginal means and adjusted pairwise contrasts were calculated. Further details on model specification and statistical procedures are provided in Paper III.

4.2.4 Paper IV – Social sham chewing

Paper IV describes the occurrence of sham chewing observed during PITs conducted with primiparous sows following weaning of their first litter. The study originated from live observations made during the late PITs described in Paper III, where rhythmic chewing movements performed in the absence of any apparent substrate in the mouth were repeatedly noted in some primiparous sows, often occurring in temporal proximity to social interactions.

The study included 81 primiparous sows from the longitudinal Study I cohort that participated in the late PITs. These primiparous sows represented different genetic lines and early and late social mixing environments. Additionally, 48 unfamiliar older sows were used as opponents in the tests. Sham chewing was coded and analysed for both primiparous sows and their older opponents, and correlations with social interactions were calculated separately for each group. An overview of the distribution of primiparous sows included in the study is provided in Figure 1.

Sham chewing was not included in the original ethogram for the PITs. However, due to its clear and recurrent expression during live observations of the tests, the behaviour was added to the ethogram during subsequent video analyses to allow a descriptive characterisation of its occurrence and surrounding social situation. Sham chewing was defined as rhythmic chewing movements performed in the absence of food material and without apparent manipulation of substrates or conspecifics.

The behaviour was coded from video recordings of the late PITs using a dedicated ethogram developed for this study. Coding focused on the presence and frequency of sham chewing in both the primiparous sow and the unfamiliar older sow, as well as its occurrence in relation to ongoing or immediately preceding social interactions. Analyses of sham chewing were primarily descriptive, reflecting the exploratory nature of the study and the limited prior knowledge regarding this behaviour in social contexts.

By documenting sham chewing as it occurred during standardised social interactions, Paper IV highlights how detailed behavioural observations can capture subtle behavioural expressions that may otherwise remain undocumented, particularly in socially complex animals. Further methodological details are provided in Paper IV.

Data handling and statistical analyses

Behavioural data on sham chewing and social interactions were extracted from video recordings of the late PITs described in Paper III and coded using BORIS (Friard & Gamba, 2016). For the first 20 minutes of each test, when most social interactions occurred, the total number of sham chewing events and the total number of social interactions were summarised across individuals. Correlations were calculated at the level of observation minute ($n = 20$).

Statistical analyses for Paper IV were exploratory and descriptive. Associations between the frequency of sham chewing and the frequency of social interactions were examined using Pearson correlation analyses, conducted separately for FPS and unfamiliar older sows, based on minute-wise aggregated frequencies. Additionally, differences in sham chewing frequency between primiparous sows and older sows were assessed using two-sample t-tests based on summarised data (sample size, mean and standard deviation), where applicable.

All statistical analyses were performed using Minitab (Minitab, LLC, 2022). Given the exploratory aim of the study and the limited prior information regarding sham chewing in social contexts across the literature, no multivariable modelling was applied. Where applicable, statistical significance was assessed using a significance level of $P < 0.05$.

4.3 Study II (Paper V)

Study II was conducted within the framework of *Ask the pig* (Fråga grisen), a national research and development project aiming to develop and validate an animal-based welfare benchmarking tool adapted to the specific conditions of Swedish pig production. The project involved close collaboration between the Swedish University of Agricultural Sciences (SLU) and the veterinary advisory company Farm & Animal Health (Gård & Djurhälsan) and encompassed on-farm welfare assessments across a wide range of commercial piglet-producing farms in Sweden.

The overall *Ask the pig* project includes multiple welfare indicators, production stages and analytical objectives, with the broader aim of supporting advisory work, certification and continuous welfare improvement through benchmarking. Paper V represents a focused scientific sub-study within this larger project, addressing a specific subset of animal-based welfare indicators and research questions relevant for group-housed gilts and sows under commercial conditions.

4.3.1 Paper V – Welfare indicators in commercial group-housed gilts and sows

Paper V examined the occurrence and distribution of visible welfare indicators in group-housed gilts and sows on Swedish commercial piglet-producing farms, with particular emphasises on skin lesions, lameness and body soiling. The study was designed as a cross-sectional observational investigation, reflecting routine commercial management without experimental manipulation.

The study was conducted on 36 commercial piglet-producing farms in Sweden between June 2022 and September 2023 and included 1447 gilts and sows assessed across four production stages: gilt rearing, gilt gestation, sow mating and sow gestation. All farms complied with Swedish animal welfare legislation, including mandatory group housing of gilts and sows during mating and gestation and the complete ban of tail docking, i.e. all pigs had intact tails.

Welfare assessments were performed through direct visual observations during on-farm visits. Skin lesions were recorded across six body regions (ears, front, middle, hindquarters, legs and tail) using a standardised scoring system adapted from the Welfare Quality® assessment protocol for pigs (Welfare Quality®, 2009). Lesion scores were converted to numerical values that reflected lesion type and severity, allowing both total lesion scores and region-specific lesion patterns to be analysed.

Lameness and body soiling were assessed using categorical three-point scales. Lameness was scored based on gait and weight-bearing ability, whilst body soiling was estimated as the proportion of the body surface covered by manure. All assessments were conducted without the animals being handled.

Information on housing and management factors was collected at the time of the visit. This included feeding system, bedding type, group size and time since the most recent regrouping. Animals were assessed in their existing social groups, and no changes to management routines were made for the purpose of the study.

This design enabled welfare indicators under practical commercial conditions to be evaluated and allowed variation in lesion patterns to be examined in relation to production stage, time since mixing, season and housing-related factors. Further methodological details are provided in Paper V.

Data handling and statistical analyses

All statistical analyses for Paper V were performed in R (R Core Team, 2024). Prior to analysis, data were checked for completeness and consistency, and descriptive summaries were generated for all welfare and housing variables.

Skin lesion outcomes were analysed as count data. Total lesion scores and region-specific lesion scores were analysed separately using generalised linear mixed models with a negative binomial distribution to account for overdispersion. For body regions characterised by a high proportion of zero values, zero-inflated model structures were evaluated and applied where supported by model fit. Zero-inflated models were retained for Middle and Hindquarters regions. Fixed effects included Animal group (gilt rearing, gilt gestation, sow mating, sow gestation), Days since mixing (≤7 days vs >7 days), Feeding system, Bedding type and Season, with Group size nested within Animal group. Season was included as a fixed effect to account for temporal variation in assessment timing. Farm nested within Season was included as a random intercept to account for clustering of animals within farms and seasonal assessment periods. Model selection and comparison were based on information criteria and biological interpretability. Model assumptions were evaluated using simulation-based residual diagnostics. Estimated marginal means and pairwise comparisons were calculated where relevant, with adjustment for multiple testing.

Lameness and body soiling outcomes were analysed descriptively. Due to the very low prevalence of moderate and severe cases and limited variation across farms and production stages, these variables were not subjected to inferential statistical modelling.

Results are presented as estimated marginal means with standard errors or as descriptive frequencies and proportions. Statistical significance was set at $P < 0.05$. Complete details of model specification and analytical procedures are provided in Paper V.

5. Main findings

Together, the studies included in this thesis investigate social behaviour and welfare-related outcomes in pigs housed under group-housing conditions. Study I examines behavioural development from early life to first parity, focusing on how early-life social environments and genetic background influence behavioural expression, social responsiveness and the occurrence of behaviour-related skin lesions under experimental conditions. Study 2 describes welfare outcomes in Swedish commercial pig production, using animal-based indicators to characterise injury patterns and other welfare-related measures in gilts and sows kept under commercial conditions. This chapter summarises the main findings from Papers I–V; detailed results are presented in the respective articles.

5.1 Study I – Social mixing environments, genetic background and behavioural strategies

Study I followed gilts with different early and late social mixing environments and genetic backgrounds from early rearing until after their first litter. Behavioural observations and paired interaction tests (PITs) were conducted at selected life stages to describe behavioural expression and social responsiveness over time. Skin lesions associated with aggressive interactions were assessed following the PIT with first-parity sows (FPSs).

5.1.1 Paper I - Behaviour, activity and social interactions during early rearing

Early-life social environment influenced how female piglets (gilts) used their environment and how behavioural patterns changed across the weaning transition. Gilts housed in access pens (APs) were observed in the neighbouring pen for 24.1% of scans during week 3 and 20.0% during week 4, and all AP gilts entered the neighbouring pen at least once. When present there, gilts spent 55.4% of the scans lying down, with no difference between genetic lines. However, pen-use patterns differed: when observed in the neighbouring pen, Swedish Yorkshire (SY) gilts spent a higher proportion of scans in the piglet corner than Dutch Yorkshire (DY) gilts (72.4% vs 58.0%).

In addition, DY gilts spent a greater proportion of scans in the neighbouring pen than SY gilts (24.0% vs 19.0%, respectively).

Across treatments, the gilts spent most scans either in the lying area (pre-weaning, with the sow present) or in the piglet corner. For AP gilts in weeks 3-4, this includes observations from both the home and neighbouring pen. Time spent in the piglet corner showed significant interactions with observation week, including both early social mixing × week and genetic line × week effects, with a marked increase directly after weaning, particularly among gilts housed in conventional pens (CPs). CP gilts also demonstrated a pronounced decrease in time spent lying after weaning, whereas AP gilts maintained more stable lying behaviour across the weaning transition. Genetic line differences were also evident, with DY gilts spending a higher proportion of time lying between weeks 3 and 6 after birth.

The occurrence of social interactions increased with age. The proportion of gilts performing nosing at least once per observation week increased from 31% in week 1 to 87% in week 10, and the proportion performing biting increased from 8% to 49% over the same period. In contrast, climbing behaviours declined from 61% of piglets in week 1 to 14% in week 10. SY gilts responded with no behavioural change to initiated social interactions more frequently than DY gilts (88.2% vs 78.9%), representing the only significant genetic line difference detected in performed or received social behaviours.

5.1.2 Paper II - Social responsiveness in paired interaction tests in young gilts

Behavioural responses during PITs varied across observation minutes and between genetic lines at both ages, whilst early social mixing influenced play behaviour at 20 weeks of age.

During the PIT conducted at 5 weeks of age, genetic line differences were most evident in exploratory behaviour. SY gilts explored pen fittings more frequently than DY gilts (1.8 vs 1.3 explorations per observation minute). Exploration increased throughout the test for both genetic lines. Proximity between the two gilts also increased after the first observation minute, with gilts spending about 60% of scans close together during the first minute, which increased to around 80% later in the test. Avoidance responses to initiated social interactions increased during the test and were most frequent during the final minute. The gilts avoided 25 % of the other pigs' attempts to interact in any way in the final minute of the test, whereas during the first minute they avoided only 8 % of social interactions. At this age, behavioural differentiation was primarily expressed through exploration and temporal changes in proximity and avoidance. No significant effects of early social mixing were detected during the five-week test.

At 20 weeks of age, clearer differentiation between groups was observed. Gilts of the SY line spent a greater proportion of time close to the opponent gilt than DY gilts (74% vs 65% of scans). Early social mixing influenced play behaviour, with gilts raised in APs being more likely to display locomotor play than gilts raised in CPs (59% vs 44% probability of play). Exploratory behaviour also differed by genetic line at this age, with DY gilts exploring pen fittings more frequently than SY gilts, and exploration of both pen fittings and floor increasing over the course of the test. Late social mixing interacted with genetic line for exploration behaviour at 20 weeks of age, whilst no main effects of late social mixing were detected for other behavioural measures.

5.1.3 Paper III - Behavioural strategies and lesion outcomes in first-parity sows

At this stage of the study, the same animals previously described as gilts are referred to as FPSs, reflecting that they had already given birth to their first litter. When the FPSs were exposed to a PIT with an unfamiliar older multiparous sow, initial contact occurred rapidly, with an average mean latency of approximately 11 seconds, and the FPS initiating the interaction in the majority of the tests (76 % of the PITs). Neither genetic line nor early or late social mixing environment influenced latency to first contact or which sow (first or multiparous) approached first.

Behavioural expression during the test differed between genetic lines and early social mixing environments, reflecting differences in behavioural strategies. FPSs reared in APs initiated more affiliative behaviours than sows reared in CPs. In contrast, genetic line was strongly associated with agonistic behavioural strategies in that SY sows initiated substantially more damaging and warning behaviours than DY sows. Late social mixing environment did not influence behaviours initiated by the FPS. The behaviour of the older sow towards the FPS also differed by genetic line of the FPS. Older sows directed more damaging behaviour and pressing towards SY FPSs than DY

FPSs, whilst neither early nor late social mixing environment of the FPS seemed to affect the behaviour of the older sow towards the FPS.

Response behaviours to interactions initiated by the older sow further reflected genetic line differences but also an early social mixing effect. SY FPSs responded more frequently with damaging and pressing behaviours to the older sows' initiated behaviour. The early social mixing experience of APs was associated with a higher likelihood of no reaction to a social interaction performed by the older opponent sow. The late social mixing environment had no consistent effect on response behaviour by FPSs.

Lesion outcomes following the PIT differed between genetic lines. SY FPSs showed a larger increase in total lesion counts and had significantly higher lesion numbers on the front, rear and legs, compared with DY FPSs. Neither early nor late social mixing environment had a main effect on lesion counts.

Several associations emerged between behaviour and lesion outcomes at the overall level. Higher frequencies of damaging and warning behaviours performed by FPSs were associated with increased lesion counts on the front of the body. In contrast, affiliative behaviour performed by the older sow was associated with reduced total lesion counts on the FPS.

Regarding FPS response behaviours, retreat and threat were associated with fewer lesions on the front of the body and fewer total lesions overall. Affiliative responses by the FPS were associated with fewer lesions on the rear body region, whereas damaging responses by the FPS were associated with increased lesion counts on the front.

Although most behaviour-lesion associations were consistent across groups, several interaction effects indicated that these relationships differed depending on genetic line and social experience. Among DY FPSs, higher frequencies of pressing were associated with increased lesion counts on the rear and in total, a pattern not observed in SY FPSs. In contrast to the overall pattern where retreat and threat were associated with fewer lesions, DY FPSs responding with retreat showed increased total lesion counts, and DY FPSs responding with threat had increased lesion counts on the front and in total. Similarly, affiliative behaviours performed by DY FPSs were associated with reduced front-body lesions, whereas affiliative behaviours directed towards DY FPSs by the older sow were associated with increased lesion counts on the front and in total. Affiliative responses by DY FPSs were also associated with increased lesion levels on the rear, a pattern not observed in SY FPSs.

Early and late social mixing environments further modified several behaviour-lesion relationships. Pressing behaviour was more strongly associated with increased lesion counts among FPSs raised without early social mixing (CP), both on the rear and in total. Likewise, when pressing was performed by the older sow, it was associated with higher lesion levels in CP FPSs compared with AP FPSs.

Although late social mixing environment had no main effect on lesion counts, it modified several behaviour-lesion relationships. Among FPSs exposed to late social mixing (MG) performance of damaging behaviour was associated with fewer lesions on the front of the body compared with FPSs from intact groups (IG). In contrast, retreat responses among MG FPSs were associated with increased lesion counts, particularly on the front of the body and in total; similarly, MG FPSs responding with threat received more lesions on the front.

5.1.4 Paper IV - Sham chewing during social challenge

Sham chewing, defined as rhythmic chewing movements performed in the absence of feed and without manipulation of substrates or conspecifics, was commonly observed during the late PIT (described in Paper III). Sham chewing occurred among all older sows (48/48) and 95% of FPSs (77/81). Although both age groups displayed this behaviour, FPSs performed sham chewing less frequently than older sows, at approximately 0.4 compared with 0.6 events per minute of observation.

Sham chewing occurred at varying time points during the test and was closely linked to social activity. The frequency of sham chewing and social interactions per minute were strongly positively correlated in both FPSs (r = 0.94, $P < 0.001$) and older sows (r = 0.90, $P < 0.001$). Mean latency to first sham chewing did not differ significantly between FPSs and older opponent sows (t-test, n.s.), although substantial individual variation was observed.

5.1.5 Genetic line, early and late social mixing environment effects - a synthesis across life stages

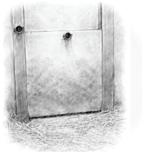
The studies included in Study I followed the same individuals across multiple life stages, from early rearing through sexual maturity and into first parity. Whilst the results were presented in detail within each individual paper, the length and longitudinal nature of the study make it informative to also consider the findings together. Summarising significant effects of genetic line (Table 1) and early (Table 2) and late social mixing environments (Table 3) across life stages allows overarching patterns to be visualised, facilitating comparisons between developmental stages and experimental conditions. This integrated overview provides a basis for the subsequent discussion, where behavioural strategies and welfare-related outcomes are interpreted in relation to long-term social experience and genetic background.

Table 1. Summary of the relative direction of the outcome when there was a significant effect[1] of genetic line (Swedish Yorkshire, SY, vs Dutch Yorkshire, DY) across life stages in Study I. Only effects with $p < 0.05$ are included as reported in Papers I-III.

	Outcome	**SY**	**DY**	**Source**
Early life (≤ *20 weeks old*)	Time spent in neighbouring pen (AP pigs, weeks 3-4)	↘	↗	Paper I
	Time spent lying (weeks 3-6; interaction with week)	↘	↗	Paper I
	Time spent in piglet corner (neighbouring pen)	↗	↘	Paper I
	Response "no reaction" to initiated social interactions	↗	↘	Paper I
	Exploration of pen fittings (PIT, 5 weeks)	↗	↘	Paper II
	Time spent close to opponent (PIT, 20 weeks)	↗	↘	Paper II
	Exploration of pen fittings (PIT, 20 weeks)	↘	↗	Paper II
As first parity sows (≈ *58 weeks old*)	Damaging behaviours initiated by FPS	↗	↘	Paper III
	Warning behaviours initiated by FPS	↗	↘	Paper III
	Damaging behaviours directed towards FPS by older sow	↗	↘	Paper III
	Pressing behaviours directed towards FPS by older sow	↗	↘	Paper III
	Damaging response behaviours by FPS	↗	↘	Paper III
	Pressing response behaviours by FPS	↗	↘	Paper III
	Total lesion gained during PIT	↗	↘	Paper III
	Lesions on front of body after PIT	↗	↘	Paper III
	Lesions on rear of body after PIT	↗	↘	Paper III
	Lesions on legs after PIT	↗	↘	Paper III
Interaction: Behaviour → lesions (first parity sows, ≈ 58 weeks old)	Pressing performed by FPS → Rear lesions	↔	↗	Paper III
	Pressing performed by FPS → Total lesions	↔	↗	Paper III
	Affiliative performed by FPS → Front lesions	↔	↘	Paper III
	Older sow affiliative towards FPS → Front lesions	↔	↗	Paper III
	Older sow affiliative towards FPS → Total lesions	↔	↗	Paper III
	FPS affiliative response → Rear lesions	↔	↗	Paper III
	FPS retreat response → Total lesions	↔	↗	Paper III
	FPS threat response → Front lesions	↔	↗	Paper III
	FPS threat response → Total lesions	↔	↗	Paper III

[1] Only statistically significant effects ($p < 0.05$) are presented, as reported in Papers I–III. Arrows indicate the relative direction of significant differences between genetic lines (SY vs DY). For outcomes involving interactions with time, arrows reflect the direction of change over the specified period rather than overall main effects. For behaviour–lesion analyses, arrows represent the direction of significant associations within each genetic line (↗ positive association; ↘ negative association; ↔ no significant association).

Table 2. Summary of the relative direction of the outcome when there was a significant effect[1] of early social mixing environment (access pens, AP, vs conventional pens, CP) across life stages in Study I.

	Outcome	 **AP**	 **CP**	**Source**
Early life (≤ 20 weeks old)	Change in piglet corner use around weaning (interaction with week)	↔	↗	Paper I
	Change in time spent lying around weaning (interaction with week)	↔	↘	Paper I
	Locomotor play behaviour (PIT, 20 weeks)	↗	↘	Paper II
As first parity sows (≈ 58 weeks old)	Affiliative behaviours initiated by FPS	↗	↘	Paper III
	No change in behaviour as response behaviour by FPS	↗	↘	Paper III
Interaction: Behaviour → lesions (first parity sows, ≈ *58 weeks old*)	Pressing performed by FPS → Rear lesions	↔	↗	Paper III
	Pressing performed by FPS → Total lesions	↔	↗	Paper III
	Older sow pressing towards FPS → Total lesions	↔	↗	Paper III

[1] Arrows indicate the relative direction of significant differences between early social mixing environments. For outcomes specified as interactions with time, arrows represent the direction of change over the relevant period within each group. For behaviour-lesion analyses, arrows indicate the direction of significant associations within each environment (↗ positive association, ↘ negative association, ↔ no significant association). Only effects with $p < 0.05$ are included, as reported in Papers I-III.

Table 3. Summary of the relative direction of the outcome when there was a significant effect[1] of late social mixing environment (mixed groups, MG, vs intact groups, IG) on behaviour-lesion associations among first-parity sows in Study I.

	Outcome	**MG**	**IG**	**Source**
Interaction: Behaviour → lesions (first parity sows, ≈ 58 weeks old)	FPS retreat response → Front lesions	↗	↔	Paper III
	FPS retreat response → Total lesions	↗	↔	Paper III
	FPS threat response → Front lesions	↗	↔	Paper III
	Damaging behaviour performed by FPS → Front lesions	↘	↔	Paper III

[1] Shown effects represent all behaviour-lesion associations that reached statistical significance ($p < 0.05$) in the analyses; no other main or interaction effects of late social mixing environment were detected. Arrows indicate the direction of significant associations within each environment (↗ positive association, ↘ negative association, ↔ no significant association). Results are based on Paper III.

5.2 Study II - Welfare-related indicators under commercial conditions

Study II assessed welfare-related indicators in gilts and sows under Swedish commercial production conditions. Skin lesions, lameness and body soiling were recorded to describe how these animal-based indicators are distributed across animals and production contexts in Sweden outside the experimental setting of Study I. Together with the experimental findings, Study II provides a broader picture of welfare-related patterns in group-housed gilts and sows.

5.2.1 Skin lesions, lameness and body soiling in group-housed gilts and sows in commercial conditions

Skin lesions were a common welfare-related finding among gilts and sows kept under Swedish commercial conditions, with lesions reported for approximately 90% of assessed animals. Lesion occurrence varied considerably between individuals, indicating that injury risk was unevenly distributed within the population.

Lesion levels differed between animal categories and production units. Overall, sows demonstrated higher lesion levels than gilts, with the highest lesion levels observed in the sow mating unit. Elevated lesion levels were also recorded in the sow gestation units, whereas the gilt units generally showed lower overall lesion levels.

Group size was associated with lesion outcomes, but the pattern differed between production units. For total lesion scores, clear group-size differences were observed in the gilt rearing units and sow gestation units, where animals housed in larger groups showed higher lesion levels than those housed in smaller groups. In contrast, in the sow mating unit, lesion levels were high across all group-size categories, with no consistent differences between group sizes. Group-size-related differences were not limited to total lesion scores but were also observed across multiple body regions, including lesions on the front, ears, middle, hindquarters and tail. In some production units, animals housed in larger groups exhibited higher lesion levels; however, these differences were production-unit specific and not consistently observed across all body regions.

When lesion outcomes were analysed by body region, lesions on the front were the most prevalent across the animal categories (74 %), followed by ear lesions (68 %) and middle-body lesions (52 %). Hindquarter lesions were observed in 35 % of the animals, whereas lesions on the legs and tail were less common (14 % each).

Lesion levels were strongly influenced by time since mixing. Animals assessed during the first week after mixing showed substantially higher levels than those assessed later (34 vs 20 lesion scores, respectively), corresponding to a 70% higher lesion burden during the immediate post-mixing period. This increase was most pronounced for lesions on the front, middle, hindquarters and legs whereas ear lesions, although common, demonstrated little variation with time since mixing.

Housing-related factors further altered lesion outcomes in a region-specific way. Lesion levels were generally higher in systems with solid lying areas compared with deep-litter systems (31 vs 23 total lesion score points, respectively). A consistent pattern across total lesions, front, ears, legs and tail indicated higher lesion levels in solid lying area systems compared with deep-litter systems. Seasonal variation was also evident, with lesion levels the highest during autumn, whilst seasonal effects were not observed for all lesion outcomes.

Compared to skin lesions, lameness and body soiling were not common. More than 99% of animals displayed a normal gait, and around 90% were classified as clean, signifying a low prevalence of overt locomotor and hygiene-related problems in the assessed commercial group-housing pens.

6. General discussion

This thesis was driven by a practical and persistent welfare challenge in modern pig production: balancing the well-established benefits of group housing, such as social contact and freedom of movement, with the management demands associated with mixing unfamiliar pigs. Group housing is widely recognised as important for enabling social interaction and behavioural needs and, in many countries, is a legal welfare requirement. However, mixing inevitably exposes gilts and sows to repeated social challenges that may result in stress, aggression and injury. In Sweden, where group housing has long been embedded in the regulatory framework, the central welfare challenge is therefore not whether sows should be housed socially, but how management practices can best support them during periods of social change. Thus, improving how gilts and sows cope with social challenges is not only a scientific question, but also a question of sustainable management in production systems where contact with unfamiliar conspecifics is unavoidable. These challenges are not unique to Sweden and are becoming increasingly relevant internationally as group housing becomes more widespread in response to evolving welfare standards and legislation.

This thesis integrates experimental and commercial production perspectives by combining longitudinal experimental data (Study I) from controlled settings with cross-sectional welfare indicator data collected under commercial group-housing conditions (Study II). Therefore, it provides both controlled experimental insight and practical relevance for understanding welfare challenges in group-housed gilts and sows.

The purpose of this general discussion is to integrate findings across the two studies whilst detailed discussions of individual results are provided in the respective published papers and manuscript (I-V). Rather than revisiting each specific result in detail, the discussion focuses on broader patterns and relationships that emerge when findings are considered across life stages and different social and management conditions.

Throughout this discussion, concepts such as resilience, social competence, coping strategies and genotype-by-environment interactions are used to support interpretation of behavioural variation across life stages and types of social challenge. These concepts help to explain why individuals may differ in their responses to regrouping or unfamiliar opponents in the experimental studies, why similar behavioural strategies may lead to different welfare outcomes and how management conditions in commercial group-housing systems influence injury risk at the population level. Importantly, they are applied to describe patterns across early rearing, PITs, and commercial group-housing assessments, acknowledging that behavioural outcomes emerge from the interaction between individual predispositions and the immediate social and physical environment.

6.1 Social experience and behavioural patterns across life stages

Social mixing experience shapes behavioural strategies rather than reducing aggression

One of the central aims of this thesis was to examine how early-life social experience influences behavioural strategies during subsequent social challenges. Across the studies included in this thesis, social experience emerged as an important environmental factor associated with variation in how gilts and sows responded to social challenges later in life. This was seen during rearing, where the early social mixing environment influenced activity patterns, space use and responsiveness around the weaning transition (Paper I). Moreover, later, during gilt development and first parity (Papers II–III), social mixing experience was reflected in differences in behavioural expressions during PITs with unfamiliar conspecifics. Notably, these effects were not expressed as a general reduction in aggression or as uniform shifts in single behaviours. Instead, social mixing appeared to influence how individuals engaged in and navigated social challenges, shaping the balance between social investigation, play, affiliation and conflict-related behaviours when exposed to unfamiliar individuals. Previous experimental work also shows that agonistic behaviour in pigs not only reflects traits such as aggression, that are influenced by genotype and early experience, but also reflects flexible adjustment to recent experience and immediate contest context (Oldham *et al.*, 2020). This interpretation reflects the conceptual perspectives introduced in the background, where the consequences of early socialisation are highly context-dependent and may be better understood in terms of altered interaction styles, coping strategies or behavioural plasticity rather than suppression of aggressive behaviour per se (Camerlink *et al.*, 2018, 2021; D’Eath, 2005; Hessel *et al.*, 2006; Jensen, 2022; Kanaan *et al.*, 2012; Salazar *et al.*, 2018).

This redistribution of behavioural responses across affiliative, avoidant and agonistic options was particularly evident in the behaviour of FPSs exposed to social challenge. FPSs with early access to additional social contact (AP) more frequently initiated affiliative behaviours when interacting with an unfamiliar older sow, whilst also demonstrating a higher likelihood of not responding to initiated interactions. Instead of signifying passivity, this pattern may reflect a greater use of non-escalatory strategies, where engagement and non-response may function as context-appropriate alternatives to confrontation (Camerlink *et al.*, 2015). These patterns can be discussed in relation to coping styles, where individuals may differ in tendencies toward proactive (more routine-based, potentially escalatory) versus reactive (more cautious, context-dependent) responses (Janczak *et al.*, 2003). Importantly, neither style is superior; their effectiveness depends on the demands and predictability of the social environment (as demonstrated in e.g. Janczak *et al.*, 2003; Krause *et al.*, 2017; Oldham *et al.*, 2020; O’Malley *et al.*, 2022; Reimert *et al.*, 2014).

It can be reasoned that in dynamic group housing systems with repeated mixing, behavioural flexibility and appropriate de-escalation may therefore be particularly relevant. In the present thesis, these patterns of increased affiliative initiation and non-response should be interpreted with consideration of the testing context. The social challenges involved standardised encounters with unfamiliar individuals under heightened social uncertainty, rather than interactions within stable groups. Within such contexts, affiliative tendencies may be expressed differently and may take the form of selective engagement and de-escalatory responding as opposed to sustained affiliative interaction. Thus, the behaviours described above are best understood as strategies for managing social risk under conditions of unfamiliarity and uncertainty, rather than as expressions of stable social preferences. This differs from affiliative behaviours in stable pig groups, where such interactions may reflect enduring partner preferences (Clouard *et al.*, 2024).

Behavioural effects persist across life stages but vary across social challenges

The relevance of early social mixing experience was evident across life stages, but primarily as differences in how behavioural responses were expressed under specific conditions, rather than as stable or uniform effects on performance of specific behaviours. Behavioural tendencies associated with early social mixing were detectable during gilt development. These remained observable when they were later exposed to social challenges as FPSs, despite substantial changes in physiological state, housing conditions and social situation.

Together, the results suggest that early social mixing experience may influence how behavioural responses are organised and deployed when animals face social challenges, instead of producing fixed or persistent behavioural traits restricted to specific behaviours or ages. This pattern challenges the assumption that early-life interventions produce stable behavioural phenotypes. Instead, it suggests that early social experience may shape behavioural flexibility and sensitivity to context, rather than fixed behavioural tendencies. Such flexibility may be particularly relevant in production systems characterised by repeated regrouping, where the ability to adjust responses over time may influence how individuals cope with social instability.

Play behaviour as an indicator of engagement and social skill development

Early differences in activity and play behaviour observed during rearing further support the interpretation above. Play is often discussed as a behaviour expressed when animals experience sufficient safety and resource availability to allocate time and attention away from vigilance and immediate competition (Spinka *et al.*, 2001), and has been linked to both positive effects and the development of motor and social skills (Horback, 2014; Newberry *et al.*, 1988). In the present work, differences in play expression are therefore interpreted cautiously, not as direct indicators of welfare but as complementary signals that early social mixing environments may influence behavioural engagement and responsiveness during social encounters with unfamiliar individuals. These findings are consistent with broader farm-animal research suggesting that early experience can shape the development of social skills, such as using social cues and selecting context-appropriate responses, that contribute to social competence across different social situations (Lee *et al.*, 2022).

Social competence and the role of early social experience in shaping behavioural strategies and welfare outcomes

In the present work, social competence is used as an interpretative perspective for patterns of behavioural adjustment rather than as a directly measured trait. Behavioural responses during the PITs were expressed in relation to the opponent's behaviour and varied depending on the type of social interaction initiated, rather than appearing as uniform response patterns across different interaction types within the test. This interactional perspective is well established within the broader literature on social stress and coping, where behavioural strategies are understood as context-sensitive responses balancing engagement, avoidance and escalation depending on the perceived risk and opportunity (Briffa & Lane, 2017; Camerlink *et al.*, 2017; Oldham *et al.*, 2021; Turner *et al.*, 2020; Weller *et al.*, 2019).

Early social experience appears to influence how animals interpret social signals and allocate behavioural responses during encounters, rather than simply altering the frequency of specific behaviours (Briffa & Lane, 2017). For example, affiliative behaviour from an unfamiliar pig may not be consistently perceived as a low-risk opportunity, particularly during standardised dyadic encounters with unfamiliar individuals in the PIT which are characterised by social uncertainty. In contrast, threatening or damaging behaviours may elicit defensive strategies prioritising withdrawal or protection over escalation. Evaluating social competence therefore requires consideration of response patterns and situational adjustment rather than reliance on single behavioural measures.

Whilst social behaviour reflects cumulative experience across development, the present findings indicate that early social mixing, compared to later social mixing, was a more consistently related factor for behavioural response patterns, associated with variation in behavioural strategies during social challenges. Later social mixing environments during rearing were not consistently associated with behavioural response patterns but were instead more closely linked to behaviour-lesion outcomes. This pattern suggests that early social mixing may primarily shape how animals adjust their behavioural responses during social challenges, whereas later social environments may influence how these behavioural strategies translate into physical outcomes such as skin lesions during the interaction. The implication is not that later social experience is unimportant, but that its welfare relevance may be expressed more strongly through accumulated outcomes than through short-term response patterns measured in standardised tests. Similar patterns have been reported in studies of early socialisation in pigs kept for commercial production, where early social contact affects later regrouping responses and welfare outcomes are often captured more clearly in cumulative lesion measures than in short-term behavioural observations. These studies, however, generally only follow pigs through a limited production phase and therefore provide a more restricted perspective than studies covering multiple life stages (Camerlink *et al.*, 2018; D'Eath, 2005; Ko *et al.*, 2020; Turner *et al.*, 2006).

Welfare implications beyond reduced aggressive behaviour

From a welfare perspective, the finding that early social mixing altered behavioural response patterns without consistently reducing lesion levels during social challenge suggests that the effects of socialisation cannot be fully understood solely in terms of reduced aggression. It can be reasoned that behavioural strategies shaped by early social experience influence how animals cope with social challenges and how conflicts unfold, without necessarily preventing injuries in short-term or highly constrained encounters. Indeed, early social experience appears to shape the behavioural toolkit available during social novelty, with implications for longer-term social functioning and how individuals may be exposed to welfare-related risks across their reproductive cycle and lifespan. Later social mixing conditions during rearing were, in contrast, less clearly reflected in short-term behavioural response patterns and more clearly associated with how social interactions translated into lesion outcomes during the PIT.

Overall, the results from the studies included in this thesis support the interpretation that both early and later social mixing environments contribute to the development of behavioural strategies that shape how gilts and sows navigate social challenges across life stages, thereby directly addressing the aim of evaluating long-term effects of social mixing environments. By focusing on patterns of behavioural adjustment instead of isolated behaviours, these findings provide a basis for understanding individual variation in social responses in group-housed systems that extends beyond both single behaviours and life stages. Furthermore, this perspective provides a basis for further consideration of how social strategies are modulated by individual background factors, and how behavioural patterns observed during social challenges are reflected in welfare-related outcomes.

6.2 Genetic background as a source of variation in social responses

Alongside examining the role of social experience, this thesis also addressed whether behavioural responses to social challenges differ between genetic lines that have been shaped under genetic selection based on performance in contrasting production and management conditions. Genetic line consistently emerged as the background factor most frequently associated with significant differences across outcomes, including early-life behavioural activity and response patterns during rearing, as well as social behaviour expressed during challenges, how FPSs were treated by older sows, and patterns of lesions and behaviour-lesion associations. These effects were, however, strongly dependent on the social situation and testing conditions. Rather than acting as a direct determinant of specific behaviours, genetic background appeared to modulate how individuals responded to social challenges. It seems to shape responsiveness and the distribution of behaviour across social strategies, consistent with variations in sensitivity, appraisal and coping rather than fixed specific behavioural outcomes. As discussed in the background section, genetic line differences may reflect indirect genetic selection related to the physical and, notably, social environments in which breeding animals have historically been evaluated and selected. At the same time, genetic differences between lines may also arise as a by-product of selection for other production-related traits, if behavioural tendencies are genetically linked to the traits actively targeted in breeding programmes (Brajon *et al.*, 2020; Kanis *et al.*, 2005). Differences in how traits are prioritised across breeding schemes, together with genotype-by-environment interactions and the specific testing conditions, are therefore likely to jointly contribute to the behavioural variation observed between lines. This is particularly relevant when lines have been shaped through genetic selection based on performance in contrasting housing and management conditions for many generations, where selection pressure related to social challenge are likely to differ (Lundeheim, 2017). The present thesis does not disentangle these mechanisms, but the findings are consistent with a multifactorial genetic background shaped by both selection history and production environment.

Context-dependent line differences beyond simple aggression rankings

Differences between genetic lines were evident across several behavioural measures, yet these differences did not simply translate into one genetic line being more or less aggressive or socially competent than the other, challenging simplified interpretations of breed or line differences in social robustness. Instead, variation between lines was most apparent in how social interactions unfolded during a challenge, including tendencies related to behavioural initiation, response patterns and the way social interactions translated into lesion outcomes. Similar context-dependent genetic effects have been reported in pigs and other social species, where genetic variation influences behavioural reactivity, stress sensitivity and coping style rather than absolute aggression levels (Camerlink *et al.*, 2013; Canario *et al.*, 2012; Turner, 2011; Turner *et al.*, 2009, 2010).

Behavioural differences between genetic lines were more pronounced under conditions of social uncertainty and challenges, such as during encounters with unfamiliar conspecifics, than under stable and familiar routine conditions. This aligns with previous findings indicating that genetic variation in social behaviour is often most visible when animals are challenged, rather than in stable social environments (Desire *et al.*, 2023; Oldham *et al.*, 2021). Interestingly, line differences were also evident regarding how older sows behaved towards the FPSs, including more damaging and pressing towards SY, suggesting that genetic line not only influenced how FPSs behaved, but also how they were perceived and treated by unfamiliar older sows. Combined, these patterns underscore the value of social challenge tests for revealing variation in behavioural patterns and strategies that may remain less visible under routine, predictable conditions.

Behaviour-lesion relationships differ across lines and welfare consequences

Higher agonistic involvement did not uniformly translate into stronger behaviour-lesion associations across genetic lines. Although SY displayed higher levels of agonistic behaviour and a higher overall lesion burden, DY showed stronger behaviour-lesion associations for several behaviours, indicating that the relationship between behavioural expression and injury outcomes differed between lines. This pattern suggests that whilst SY was more frequently involved in potentially injurious interactions, DY may, in certain behavioural situations, have shown a stronger association between specific behaviours and lesion outcomes. Thus, genetic line differences were not only expressed in how often animals engaged in social conflict, but also in how behavioural interactions were linked with physical welfare outcomes. Regarding socialisation, socialised piglets have been seen to fight more swiftly after weaning. However, they also formed dominance hierarchies faster which in turn suggests that they have better social skills (D'Eath, 2005). One interpretation can be that line differences may reflect differences in how conflicts unfold and terminate; however, the present data do not allow direct inference about 'social skills' per se, and this remains speculative.

Genetic background shapes response patterns and coping style variation

The findings of this thesis suggest that genetic background influences how animals respond to the behaviour of others as well as how they initiate social interactions. Response patterns differed depending on both genetic line and the type of behaviour expressed by the opponent sow, underscoring the interactional nature of social behaviour. These findings are consistent with literature describing genetic variation in coping styles, where individuals differ in their propensity toward proactive or reactive strategies, with consequences for how they handle social stress and conflict (Janczak *et al*., 2003; Reimert *et al*., 2014). This also aligns with the genotype-by-environment interaction perspective, where line differences are expressed differently depending on the social and management conditions within the production system. Standardised social challenge tests may therefore reveal genetic line differences that remain less visible under routine or more predictable conditions.

Genetic line differences were accompanied by substantial variation between individuals within each line, indicating that genetic background influenced behavioural tendencies at the population level without determining behavioural outcomes for individual animals. Line-related effects were evident across multiple outcomes, yet were not uniform across behaviours, life stages or social situations, and often only emerged under specific social conditions or as interaction patterns rather than consistent main effects. Consequently, genetic line should be interpreted as a source of probabilistic variation rather than a fixed indicator of social robustness or coping capacity in group-housed systems.

Welfare implications depend on social and management interactions

From a welfare perspective, the present results indicate that genetic background may influence vulnerability or resilience to social challenges, not by eliminating conflict, but by shaping how pigs engage with, withdraw from or otherwise cope with social challenges such as mixing, regrouping or other changes within the social group. Such differences may have implications for injury risk, stress exposure, and long-term welfare, particularly in systems where animals are repeatedly exposed to changes in group composition and varying social dynamics (Greenwood *et al*., 2014; Jang & Oh, 2022; Spoolder *et al*., 2009). However, the expression of genetic predispositions appears to be strongly dependent on the social and environmental conditions, reinforcing the importance of management practices that interact constructively with genetic variation.

Selection history and production environment shape behavioural outcomes

A fundamental principle in animal breeding is that genetic selection should be based on performance evaluations in environments that resemble those in which the animals and their offspring are expected to perform in. From this perspective, genetic differences in social responses should be interpreted with consideration of the historical environments under which genetic selection has occurred. When genetic lines are developed under different housing, management and social conditions, the behavioural strategies that are genetically favoured or tolerated by selection may differ accordingly. Moreover, genetic effects are acquired over many generations and in cases where adjustments or a new direction in genetic change is preferred it can take numerous generations of breeding to achieve the preferred change. This has important implications for the interpretation of genetic line differences in international breeding programmes, where the same genetic material is expected to perform across a wide range of production systems. Whilst breeding companies aim to develop robust and adaptable animals (i.e. genetic plasticity), variation in social housing, group stability and management practices may interact with genetic predispositions in ways that are not fully predictable. The present findings illustrate that genetic background does not act independently of the social situation in which behaviour is assessed, and that behavioural responses emerging from social challenges may signify mismatches or alignments between the selection history and current production environment.

Overall, the findings of this thesis support a nuanced interpretation of genetic background as a source of variation in social responses rather than as a direct determinant of welfare outcomes. Genetic line influences how social challenges are perceived and managed, interacting with social experience and context to shape behavioural strategies. This perspective moves beyond simple genetic comparisons and highlights the importance of integrating genetic background with environmental and experiential factors when interpreting social behaviour and welfare in group-housed sow systems.

6.3 Behaviour - lesion relationships and welfare interpretation

A further central question addressed in this thesis concerns how behavioural expression during social interactions relates to welfare-relevant outcomes, with skin lesions used as a practical indicator of injury risk arising from damaging social interactions. Across the studies included in this thesis, relationships between behavioural expression and lesion outcomes were evident but complex, underscoring the need for cautious interpretation of both types of assessment. Behaviour during social challenges was associated with injury outcomes under some conditions, yet these associations were neither uniform nor direct. Instead, lesions reflected cumulative exposure to social risk over time rather than immediate behavioural expression in a given moment or a single aggressive act. This distinction is crucial for interpreting lesion data in relation to short-term behavioural observations.

Skin lesions reflect multiple interaction types and are influenced by environmental and management factors

Skin lesions are widely used as welfare indicators for group-housed pigs because they are relatively straightforward to record and provide an integrated measure of damaging social interactions (Burfoot *et al*., 1995; Greenwood *et al*., 2014; Spoolder & Vermeer, 2015; Tönepöhl *et al*., 2013). In this sense, lesion outcomes may partly reflect individual differences in resilience to repeated social challenges, expressed as accumulated injury risk over time rather than as responses to isolated aggressive events. However, lesion outcomes are shaped by multiple interacting factors, including the frequency, intensity and reciprocity of social interactions, as well as environmental conditions such as space allowance, group stability and housing design (Greenwood *et al*., 2014; Spoolder *et al*., 2009; Spoolder & Vermeer, 2015). The body-region-specific patterns observed further illustrate this complexity, as lesions on different body areas likely reflect distinct interaction types and exposure processes and not a single underlying behavioural mechanism (Turner *et al*., 2006). For example, lesions on the front and shoulder region are commonly associated with reciprocal fighting during hierarchy formation. In contrast, lesions on posterior regions are often interpreted as signifying non-reciprocal biting, displacement or restricted avoidance opportunities, although substantial overlap exists and patterns remain context dependent (Tönepöhl *et al.*, 2013; Turner *et al.*, 2006, 2009). Thus, similar behavioural strategies may result in different injury outcomes depending on the social and physical conditions.

In the present work, behavioural strategies associated with tolerance, withdrawal or selective engagement did not consistently translate into reduced injury risk. This was particularly apparent in short-term or highly constrained social encounters, where non-escalatory responses could coexist with social contact and physical damage. Such findings are consistent with previous studies which show that avoidance or submissive behaviours do not necessarily prevent injury when social uncertainty remains high or when opportunities for spatial separation are limited (Anil *et al.*, 2006; Arey & Edwards, 1998; Spoolder *et al.*, 2009; Spoolder & Vermeer, 2015; Verdon *et al.*, 2015). Conversely, more active engagement did not always result in higher lesion scores, especially when conflicts were brief or involved ritualised interactions rather than prolonged aggression. Together, these patterns indicate that injury risk cannot be inferred directly from behavioural style alone.

A central conceptual contribution from this thesis is that lesion outcomes should be interpreted as outcome-based indicators reflecting realised exposure to welfare risks and not direct reflections of behavioural motivation. Lesions may accumulate on individuals that frequently engage in social interactions, regardless of whether those interactions are affiliative, neutral or agonistic. Accordingly, behavioural patterns that appear socially tolerant or affiliative may still be associated with increased injury risk if they involve high levels of physical contact. Separating "how animals behave" from "what welfare outcome follows" is therefore essential for accurate welfare interpretation. In the present work, this was reflected in the fact that social-environmental differences during later rearing were detectable in how social interactions translated into lesion outcomes, even when corresponding differences between groups in short-term response patterns during standardised challenges were limited.

The social environment during later rearing emerged as a key factor for lesion outcomes, despite showing limited association with behavioural response patterns in standardised social challenge tests. Differences in late social mixing environment were associated with variation in how behavioural interactions translated into lesion outcomes, suggesting that features of the rearing environment influenced cumulative injury risk through mechanisms not captured by short-term behavioural assessments. This finding highlights that social environments may shape welfare outcomes even when effects on momentary behavioural strategies are subtle or absent, reinforcing the importance of considering the later social mixing environment when interpreting lesion data.

These results align with observations from commercial group-housed systems, where lesion prevalence reflects prolonged exposure to social instability, competition and environmental constraints rather than isolated behavioural events (Camerlink *et al*., 2014; D'Eath, 2005; Turner *et al*., 2017). Lesion data therefore provides critical information about cumulative welfare challenges, but do not, in isolation, reveal the behavioural processes underlying injury accumulation. Behavioural observations, in contrast, offer insight into social strategies and coping mechanisms, yet may not reliably predict injury outcomes without considering social and environmental conditions and exposure duration.

Together, the behaviour-lesion relationships observed in this thesis emphasise the value of integrating both behavioural and lesion-based measures in welfare assessment. Behavioural strategies shaped by early social experience, genetic background and social situation influence how social challenges are navigated, but their welfare consequences depend on cumulative exposure and environmental conditions over time. Recognising this distinction is essential for interpreting welfare indicators and for understanding how management and rearing environments contribute to injury risk in group-housed sow systems.

6.4 Interpreting behavioural and lesion-based indicators of animal welfare across experimental and commercial settings

Another overarching aim of this thesis was to integrate behavioural observations and outcome-based welfare indicators to improve the interpretation of welfare in group-housed gilts and sows. The studies included in this thesis draw on multiple types of data to assess social behaviour and welfare in gilts and sows, including behavioural observations, standardised social challenge tests and lesion-based welfare indicators collected under both experimental and commercial conditions. Together, these approaches provide complementary perspectives on social functioning and welfare, but they also fundamentally differ in the aspects of social life that they capture. Interpreting the findings therefore requires careful consideration of the strengths, limitations and underlying assumptions associated with each type of measure.

A central premise for interpreting the findings of this thesis is that no single measure captures "welfare" in its entirety but rather reflects different temporal and functional dimensions of the animal's experience. Within this interpretative perspective, a useful starting point for understanding social aspects of pig welfare in commercial systems is the mismatch between the social ecology from which pig social behaviour evolved and the social conditions imposed by modern production. Under natural conditions, female pigs typically form stable, matrilineal groups where most interactions occur between familiar individuals, hierarchies are reinforced through recognition and prior experience, and spatial structure allows avoidance and predictable use of resting and foraging areas (D'Eath & Turner, 2009; Graves, 1984; Jensen, 2022; Kaminski *et al.*, 2005; Podgórski *et al.*, 2014). In contrast, commercial group housing often involves repeated mixing of unfamiliar animals, restricted or contested resources (most notably feed, but also space, resting areas and access points), and pen designs that constrain avoidance options, creating social instability and uncertainty that does not resemble the stability of natural group living (Arey & Edwards, 1998; Greenwood *et al.*, 2014; Verdon *et al.*, 2015). Within this context, welfare risk is not solely a function of whether animals are group-housed, but of how instability in the social dynamics and competitive pressure are structured across the production cycle.

Behavioural measures and social challenge tests capture short-term strategies under uncertainty

Behavioural observations, whether conducted during early life or in controlled test situations, provide direct insight into how animals interact with their social environment. Such measures are well suited to capturing behavioural strategies, responsiveness to social cues and short-term adjustment to social uncertainty. However, behavioural data are inherently situation- and time-specific. They reflect what animals do in a given situation, but not necessarily the cumulative consequences of repeated interactions over longer periods. Therefore, behavioural measures alone cannot be assumed to provide a complete representation of longer-term welfare outcomes in group-housed systems, particularly when observations are limited to short windows or specific social configurations.

Standardised social challenge tests, including the PITs used in this thesis, occupy a specific position within this spectrum of approaches. By exposing animals to unfamiliar social situations under controlled conditions, these tests allow behavioural responses to social uncertainty to be studied whilst limiting confounding variation in environment and group composition. This standardisation represents a methodological strength, enabling comparisons across individuals, treatments and life stages. At the same time, such tests simplify social complexity. They do not capture longer-term processes such as hierarchy formation, coalition behaviour or cumulative social learning, nor do they allow animals to fully employ spatial avoidance strategies that may be available in commercial group-housing systems.

Thus, the value of social challenge tests does not lie in their ability to replicate everyday social life, but in their capacity to reveal how individuals respond when social expectations are disrupted. Responses observed under these conditions reflect behavioural strategies deployed during uncertainty rather than routine social functioning. Acknowledging this distinction is essential for interpreting behavioural differences identified in experimental tests and for avoiding overgeneralisation of group-level dynamics in production systems. This distinction reflects the background discussion on the role of standardised tests as tools for probing behavioural strategy rather than everyday behaviour.

Lesions and other welfare indicators reflect cumulative exposure rather than behaviour alone

Lesion-based welfare indicators provide a fundamentally different type of information. Rather than capturing behaviour directly, lesions reflect realised exposure to damaging interactions over time. As such, lesion outcomes integrate multiple dimensions of social experience, including interaction frequency, intensity and duration, as well as environmental and management-related constraints. This cumulative nature renders lesion measures highly relevant for welfare assessment, particularly within systems where animals are repeatedly exposed to social challenges. However, lesion data do not reveal the behavioural processes underlying injury accumulation and cannot distinguish between different behavioural strategies that may lead to similar outcomes.

As outlined in the Background (Sections 2.1–2.3), animal welfare in group-housed sows cannot be captured by a single outcome, as welfare reflects multiple interacting dimensions shaped by both social and physical environments. Beyond skin lesions, welfare assessment in commercial herds also relies on indicators that capture dimensions not directly related to social conflict. Lameness reflects locomotor health and pain, and may arise from a combination of flooring characteristics, claw health, body condition and the cumulative consequences of social pressure (e.g. displacement from preferred lying areas or altered activity patterns) (Heinonen *et al.*, 2013). Body soiling largely reflects environmental and pen-functional factors (e.g., thermal comfort, flooring and space allowance) rather than social interactions per se, as pigs may prioritise thermoregulation over keeping their resting area clean under suboptimal conditions (Nannoni *et al.*, 2020). Including multiple indicators therefore allows welfare to be interpreted as a multidimensional outcome shaped by interacting social and physical environments, rather than as a single continuum from "aggression" to "no aggression". In Study II of this thesis, overt lameness and body soiling were rare, with the vast majority of animals displaying a normal gait and being classified as clean. This low prevalence should not be interpreted as evidence that locomotor or hygiene-related problems are absent or unimportant in Swedish sow production. Indeed, several reports from Swedish commercial herds indicate that lameness and leg problems constitute a substantial welfare challenge at the population level (Andersson *et al.*, 2016; Engblom *et al.*, 2008; Hidås *et al.*, 2025). The low prevalence observed here may partly reflect the specific sampling setting of the study, where animals were assessed whilst present in commercial group-housing pens and where individuals with pronounced locomotor problems or poor general condition are typically removed from these systems and placed in hospital pens for treatment. Under the surveyed conditions, skin lesions therefore emerged as the most prominent welfare indicator within group-housed pens, whilst lameness and body soiling were less informative in this specific observational setting.

The present findings illustrate how behavioural and lesion-based measures may yield partially divergent signals without being contradictory. Behavioural strategies observed during social challenges did not consistently predict lesion outcomes, and later social environments influenced injury patterns even when associations with behavioural responses in standardised tests were limited. Such patterns highlight the risk of interpreting any single measure as a direct proxy for welfare and emphasise the need to consider both behavioural processes and cumulative outcomes when evaluating welfare for sows in group-housing systems. This integrative interpretation directly builds on the behaviour-lesion relationships discussed in Section 6.3.

Commercial herd data provide external validity but require cautious interpretation

Data collected under commercial conditions, as was the case in Study II, add an additional interpretative layer. In commercial herds, skin lesions were recorded in approximately 90% of the observed animals, with considerable variation between individuals, illustrating both the scale of social injury exposure and the uneven distribution of welfare risk within populations. This illustrates the scale and variability of welfare outcomes under real production conditions, highlighting patterns that cannot be fully captured through controlled experimental designs alone. Importantly, associations between group size and lesion outcomes were dependent on production stage. Group size effects were evident in gilt rearing and sow gestation units, whereas lesion levels in the sow mating unit were high regardless of group size, demonstrating that ‘group size’ cannot be interpreted as a uniform welfare risk factor across production stages. At the same time, commercial herd data are shaped by a wide range of uncontrolled factors and do not allow causal inference in the same way that experimental studies do. Their primary strength lies in external validity and relevance to real-world production systems, complementing the experimental insights generated under controlled conditions.

Overall, the approaches used in this thesis capture different temporal and functional aspects relevant to welfare assessment. Behavioural measures reflect how animals respond to social uncertainty and engage with their social environment in the moment, whereas lesion, lameness and hygiene outcomes indicate realised welfare consequences and accumulated constraints over time. Notably, the absence of overt welfare compromise (e.g. injuries or other observable problems) should not be interpreted as good welfare per se. Demonstrating good welfare would require studies specifically designed to measure indicators of good welfare. Interpreting behavioural and outcome-based measures together therefore allows welfare to be understood as a dynamic process shaped by behavioural strategies, environmental conditions and cumulative exposure, rather than as a binary state or a single outcome measured at one point in time.

6.5 Sham chewing as a potential indicator of behavioural regulation

An unexpected finding in Study I was the frequent occurrence of sham chewing, defined as chewing movements without any apparent substrate in the mouth. In light of this finding, sham chewing was scrutinised and interpreted as a behaviour with the potential to reflect how animals regulate arousal, frustration or motivational imbalance. This section therefore complements the preceding analyses of social behaviour and lesion outcomes by addressing a different, but equally important, dimension of welfare.

In Paper IV, sham chewing was observed in nearly all older sows and most FPSs during the PITs, with higher frequencies reported for older sows. Although sham chewing as a distinct behaviour within a social context has received limited scientific attention among pigs, repetitive oral behaviours have been more broadly discussed in the literature in relation to stereotypic behaviour, motivational frustration, feeding-related arousal and coping processes in farm animals (Appleby & Lawrence, 1987; Li & Gu, 2024). However, the behaviour documented here differs from stereotypic oral behaviours typically described in the literature. In the present study, sham chewing was recorded descriptively, without assumptions regarding pathological repetition or impaired behavioural control, and was therefore not classified as a stereotypy. Instead, it was treated as a distinct oral behaviour occurring in a socially and behaviourally active context. Sham chewing was positively associated with overall social activity during the test. Nevertheless, its functional significance remains unclear and warrants further targeted investigation.

To interpret these observations, it is important to consider the social situation in which sham chewing was expressed. In contrast to stereotypic oral behaviours typically described in the literature, sham chewing in the present study did not appear as a repetitive behaviour expressed in isolation or under conditions of behavioural restriction. Instead, it was consistently observed during socially arousing situations, often when sows were oriented towards and visually engaged with one another. This context-dependent expression suggests that sham chewing may be linked to the regulation of arousal during social engagement, rather than reflecting chronic frustration or impaired behavioural control. However, it cannot be ruled out that the behaviour may also play a role in social signalling, and the present study does not allow these alternatives to be disentangled.

Taken together, the observations of sham chewing in Paper IV underscore the presence of a behavioural expression that is consistently embedded in socially arousing encounters yet remains poorly characterised in terms of function. By documenting sham chewing in a defined social test context and demonstrating its association with social activity, this thesis contributes descriptive evidence that such behaviours may form part of the behavioural repertoire expressed during social engagement rather than under conditions of behavioural deprivation (as stereotypies). Although the present data do not allow conclusions to be drawn regarding functional role or welfare significance, the findings underline the importance of considering behavioural expressions that fall outside conventional categories of aggression, avoidance or injury. Sham chewing therefore illustrates how welfare-relevant behavioural regulation may be expressed in subtle and situation-dependent ways, but this requires further targeted investigation.

6.6 Implications for sow welfare, longevity and sustainability

Toward a nuanced, process-oriented understanding of welfare across the reproductive lifespan

In line with the overarching aims of this thesis, the findings synthesised here contribute relevant knowledge for improving welfare and sustainability in commercial group-housed sow systems by enhancing the understanding about individual variation in behaviour and welfare-related outcomes. Rather than identifying single determinants of good or bad welfare, the results highlight the importance of behavioural strategies, cumulative social exposure and contextual factors across the reproductive lifespan. Together, these insights support a shift from simplified expectations of welfare interventions toward a more nuanced, risk- and process-oriented understanding of social functioning in group-housed gilts and sows.

Early social experience and management interventions as drivers of behavioural flexibility and welfare risk

A key implication concerns the role of social mixing experience in shaping later social functioning. The present findings suggest that early social mixing does not uniformly reduce aggression but may influence how gilts and sows assess and respond to social challenges across life stages. From a welfare perspective, this indicates that early-life social mixing environments can contribute to the development of behavioural repertoires that support flexible coping rather than conflict avoidance. Such flexibility may be particularly relevant in systems characterised by repeated social disruption, such as those involving mixing at weaning, gilt introduction or regrouping of sows. Potential welfare-relevant effects of early socialisation may therefore be realised not through immediate reductions in injury, but through altered behavioural responses that influence patterns of social interaction and exposure to social risk over time.

These findings also have implications for expectations placed on management interventions. The absence of a simple relationship between affiliative or tolerant behaviour and reduced injury risk cautions against assumptions that behavioural changes alone will translate into reduced welfare risks. Management strategies aimed at reducing welfare risks and constraints should therefore consider both behavioural processes and the structural conditions in which social interactions occur, including space availability, group stability and opportunities for avoidance. Interventions that support behavioural flexibility may need to be combined with environmental design and management practices that reduce cumulative exposure to social risk to achieve meaningful and sustained reductions in welfare compromise.

This implies that welfare improvement in group-housed systems is likely to require layered solutions: management that minimises avoidable social instability (e.g., how and when animals are mixed), pen designs that facilitate spatial avoidance and escape opportunities, and monitoring systems that identify high-risk periods and vulnerable individuals early, particularly around gilt integration and the first reproductive cycle. Commercial data further emphasised the importance of timing, with lesion levels peaking during the first week after mixing, which has been documented in several studies (e.g. Arey, 1999; Greenwood *et al.*, 2014; Moore *et al.*, 1993; Zurbrigg & Blackwell, 2006). Lesion prevalence was particularly high in the sow mating unit, where elevated lesion levels were observed across group sizes, highlighting this phase as a critical management window for welfare risk, given the high degree of social reorganisation associated with this stage. Lesion risk was further shaped by physical environment and season, with higher lesion levels observed in systems with solid lying areas compared with deep-litter systems, and a pronounced peak during autumn, underscoring that welfare risk profiles emerge from the interaction between social management and housing conditions. This interpretation aligns with the present results which show that behavioural strategies observed during standardised challenges did not consistently predict lesion outcomes, whilst later social environments were more clearly associated with cumulative injury patterns.

Genetic background and the need for integrated breeding and management approaches

Genetic background emerged as an additional source of variation in social responses, with implications for breeding and selection strategies. Rather than identifying genetic lines as inherently more or less aggressive, the results indicate that genetic background modulates how individuals respond to social uncertainty and the behaviour of others. This suggests that selection for social robustness may benefit from focusing on response patterns and coping strategies rather than on single behavioural traits or injury outcomes. At the same time, the substantial within-line variation observed underscores that genetic selection alone is unlikely to eliminate welfare challenges associated with social housing and should be considered as one component within a broader management strategy. This is consistent with the present findings, where genetic line effects were primarily expressed in interaction with the social situation rather than as uniform main effects on injury or behaviour.

Bridging experimental and commercial perspectives on sow welfare

The observed dissociation between behavioural strategies and lesion outcomes further highlights the importance of integrating multiple welfare indicators. Lesions provide critical information about realised welfare risks and cumulative exposure to damaging interactions, but they do not capture the behavioural processes underlying injury accumulation. Behavioural observations, in contrast, offer insight into social strategies and coping mechanisms, yet may not reliably predict longer-term outcomes without consideration of exposure duration and social and environmental conditions.

For welfare assessment and benchmarking, understood as the identification and comparison of welfare-related risks rather than the achievement of good welfare, this implies that combined approaches rather than single indicators are better suited to capture the multifaceted nature of welfare in group-housed systems.

It is also important to acknowledge the temporal and structural scope of the behavioural assessments underlying these interpretations. Although individuals were followed across extended periods and multiple life stages, behavioural data were derived from standardised social challenge tests of limited duration. These tests were designed to isolate and characterise behavioural responses to social novelty under controlled conditions, as opposed to capturing the full complexity of social interactions occurring in stable or newly mixed groups over time. As such, they provide insight into how animals respond to an unfamiliar individual, but not the broader interaction networks, feedback processes and cumulative social dynamics that emerge during group mixing in commercial systems. Consequently, the behavioural differences observed between social mixing environments and genetic lines should be interpreted as indicative of underlying response tendencies rather than as comprehensive representations of social functioning at the group level. To fully understand how developmental experience and genetic background shape welfare outcomes in practice, future work should combine controlled social challenge tests with observations of group-level interaction patterns during and following mixing events. Such approaches would allow the behavioural mechanisms identified here to be evaluated within the complex social environments in which welfare risks ultimately arise.

Insights from commercial herds reinforce the relevance of this integrated perspective. The prevalence and distribution of lesions observed under commercial conditions illustrate the scale and variability of welfare challenges faced by gilts and sows in practice. These findings emphasise that welfare outcomes emerge from the interaction between individual characteristics, social experience and system-level management. Sustainable improvements in sow welfare therefore require approaches that are robust across diverse production systems rather than optimised for specific experimental conditions.

Study II further demonstrates that welfare challenges in group-housed systems are not restricted to skin lesions. Variation in lameness and body soiling highlights that housing and management influence welfare through multiple pathways, including locomotor strain, hygiene, thermal comfort and pen function. From a practical perspective, this supports the use of combined welfare monitoring where lesion scoring is interpreted alongside locomotion and hygiene assessments, particularly during high-risk periods in the production cycle. Such integrated monitoring is also relevant for sustainability, as locomotor problems and poor general condition are common contributors to reduced productivity and premature removal in commercial herds (Andersson *et al*., 2016; Engblom *et al*., 2008; Hidås *et al*., 2025).

Longevity, resilience and sustainable welfare in modern group-housed systems

From a longevity and sustainability perspective, the results suggest that repeated exposure to social challenges should be considered as a central welfare risk factor across the sow's productive life, and particularly during early parity transitions. Behavioural strategies that influence how individuals engage with social challenges may not only affect short-term welfare-related indicators, but also cumulative stress exposure and injury risk, with potential consequences for health, productivity and culling decisions. Improving how animals cope with unavoidable social challenges may therefore contribute to longer productive lifespans and reduced unplanned removals, aligning welfare goals with economic and sustainability objectives.

From a resilience perspective, repeated regrouping, competition and environmental variation can be viewed as recurrent challenges that potentially differ in how intensely they disrupt individuals and how quickly individuals return to baseline functioning. Thus, variation in behavioural strategies and injury risk across life stages may reflect differences in resilience (i.e., reaction norms), rather than differences in exposure to social challenges alone.

The early reproductive period may be particularly important in this respect. Both national and herd-level datasets indicate that early parity animals are overrepresented among unplanned removals in group-housed systems, suggesting that the transition into the breeding herd constitutes a critical window where social and physical challenges may exceed the coping capacity for some individuals (Engblom *et al*., 2007; Hidås *et al*., 2025; Moeller & Stalder, 2024; Wallenbeck *et al*., 2024). Although the present thesis did not quantify culling outcomes directly, the life-stage perspective applied here offers insight into potential pathways through which social challenge exposure could plausibly contribute to longer-term vulnerability and reduced retention in commercial herds.

At a broader level, the findings of this thesis have relevance beyond the Swedish production context. As group housing becomes increasingly widespread in response to evolving welfare standards and legislation, understanding how social experience, genetic background and management interact to shape welfare outcomes is vital. The present work underscores that group housing, although fundamentally beneficial for welfare, does not in itself guarantee positive outcomes. Attention must instead be directed toward how social challenges are managed across life stages and how systems can be designed to support adaptive social functioning over time.

Overall, the implications of this thesis point toward a holistic approach to sow welfare that integrates developmental experience, genetic variation and management practices. By moving beyond simplified expectations of single-factor solutions, these findings support strategies aimed at enhancing behavioural flexibility, thereby reducing cumulative social risk and promoting sustainable welfare outcomes throughout the reproductive lifespan of group-housed gilts and sows, recognising that welfare not only depends on how animals are housed, but also on how well individuals are equipped to cope with the social demand of modern group housing systems.

6.7 Methodological considerations and limitations

The findings presented in this thesis are based on a combination of experimental and observational approaches applied across different life stages and production systems for gilts and sows. This methodological diversity represents a major strength, allowing social behaviour and welfare-related outcomes to be examined from complementary perspectives. At the same time, it introduces important considerations regarding inference, generalisability and interpretation that warrant explicit reflection.

Longitudinal design enables life-stage continuity but involves practical constraints

A central methodological feature of Study I was the longitudinal follow-up of the same individuals from early rearing throughout gilt development and into first parity. This design allowed for an assessment of how early-life social environments and genetic background were associated with later behavioural strategies and outcomes relevant to welfare risk, such as injury patterns and behavioural responses during social challenges. Longitudinal designs are particularly valuable for addressing questions about developmental continuity, but they also involve practical constraints. Attrition across life stages and unequal sample sizes between analyses inevitably reduced statistical power for some comparisons and limited the scope for detecting subtle effects. Whilst this may have constrained precision, the consistency of patterns observed across outcomes and life stages supports the robustness of the main conclusions.

The experimental components of the thesis relied heavily on behavioural observations and standardised social challenge tests. Behavioural data provide valuable information about social strategies, responsiveness and coping, but they are inherently situation dependent. Observations capture behaviour expressed under specific conditions and time frames and thus should not be interpreted as fixed traits or direct proxies for long-term welfare. Rather, they reflect how individuals respond to defined social situations at specific points in time. This is particularly relevant when comparing behaviour across developmental stages, where physiological state, motivation and social role may differ substantially. The present work therefore interprets behavioural measures as indicators of situational strategies rather than stable individual characteristics. Similarly, the interpretation of non-social behaviours such as sham chewing is constrained by limited knowledge of functional significance, highlighting the need for cautious inference and further research.

Standardised social challenge tests, including PITs, were used to examine responses to unfamiliar conspecifics under controlled conditions. Such tests offer important methodological advantages by reducing environmental variability and allowing individual responses to be compared across treatments and life stages (Ambruosi *et al.*, 2024; Murphy *et al.*, 2014). However, they also simplify social complexity. Dyadic encounters cannot capture group-level processes such as hierarchy formation, coalition dynamics or cumulative social learning, nor do they fully reflect the spatial and social options available in commercial group-housing systems. At the same time, the dyadic structure allows the interaction between two individuals to be examined in detail without the influence of additional group members, which may otherwise alter or interrupt ongoing interactions. Another advantage of dyadic tests is that the two interacting individuals can be selected according to predetermined characteristics, such as treatment background or age, which would be difficult to control in larger group settings where interaction partners cannot be predetermined. Consequently, the behavioural responses observed in these tests should be interpreted as responses to experimentally induced social uncertainty rather than as direct representations of everyday social functioning.

Because PITs in this thesis were conducted at different ages, they also allowed comparisons of how relative differences between treatments changed across developmental stages. The short-term behavioural responses analysed in Paper II reflect acute reactions to an unfamiliar and unexpected situation, with minimal opportunity for habituation, learning or adjustment. Such acute tests are therefore likely to capture rapid, short-latency responses driven by immediate appraisal of social uncertainty, rather than more elaborated behavioural strategies that may emerge when individuals are given time to assess, adapt and regulate their behaviour. In contrast, longer observation periods, including repeated social interactions or extended challenge tests, allow for behavioural modulation, experience-dependent adjustment and the expression of more integrated coping strategies. Different tests reveal different layers of behavioural response, from immediate, reflex-like reactions to more contextually embedded social strategies. Thus, interpreting findings across studies requires explicit consideration of acute responsiveness versus behavioural organisation over time. Together, these complementary approaches provide a picture of how gilts and sows respond to social challenges across life stages and social and environmental conditions.

Lesion-based welfare indicators constituted a key outcome measure across several studies and provided an integrated assessment of realised exposure to damaging social interactions. Lesions are widely used in welfare assessment due to their practicality and relevance, but they are influenced by multiple interacting factors. Environmental conditions, group composition, space allowance and management practices all contribute to lesion development, and similar behavioural strategies may result in different injury outcomes depending on social and environmental conditions and exposure duration. In this thesis, lesions are therefore interpreted as indicators of cumulative welfare risk rather than as direct reflections of behavioural motivation or intent. This distinction is critical to avoid overinterpreting lesion outcomes as purely markers of aggression or overall welfare state.

An important methodological insight emerging from this work is the limited correspondence between behavioural responses observed in short-term tests and longer-term lesion outcomes. Later social environments during rearing were associated with lesion prevalence and distribution despite demonstrating limited associations with behavioural response patterns in standardised tests. Age-related changes in social behaviour across development may also contribute to this pattern, as behavioural responses and welfare outcomes were assessed at different life stages. This highlights that welfare-relevant outcomes may be shaped by prolonged exposure to social and environmental conditions that are not fully captured by momentary behavioural assessments. The combination of behavioural and lesion-based measures is therefore essential for a more complete understanding of welfare, but it also requires careful interpretation across different time frames and social and environmental conditions.

Interpreting behavioural and cumulative welfare indicators across experimental and commercial settings

Study II provided welfare data from commercial group-housed systems, offering high external validity and relevance to real-world production conditions. However, the observational nature of this data limits causal inference. Associations identified in commercial herds reflect the combined influence of management, housing, genetics and environmental factors, many of which cannot be disentangled. Rather than being viewed as a limitation, this complementarity between experimental control and commercial relevance strengthens the thesis by situating mechanistic findings within a broader production context. Nevertheless, conclusions drawn from commercial data should be interpreted as descriptive and hypothesis-generating rather than causal.

Across Papers I-III, genetic line was treated as a source of structured variation rather than as a deterministic predictor of behaviour or welfare. Whilst genetic comparisons provide valuable insight into population level tendencies, substantial within-line variation was observed, underscoring the importance of avoiding overgeneralisation. Genetic background should therefore be interpreted as one of several interacting factors that shape social behaviour and welfare-relevant outcomes, rather than a standalone explanatory variable.

Strengths and limitations of an integrated welfare assessment approach

Taken together, the methodological considerations outlined above emphasise that no single measure or approach can fully capture the complexity of social behaviour and welfare in group-housed gilts and sows.

The strength of the present thesis lies in its integration of multiple observation types across life stages and contexts, including behavioural observations, standardised social challenge tests, lesion-based indicators and welfare data from commercial herds. Each of these approaches captures distinct temporal and functional dimensions of social functioning and welfare-relevant outcomes. On the other hand, the limitations inherent to each method highlight the importance of cautious interpretation, avoidance of oversimplified conclusions and recognition of the boundaries which the findings are applicable within. When interpreted alone, individual measures provide only partial insight. When considered together, they allow a more nuanced understanding of how social experience and genetic background shape behavioural strategies and cumulative welfare risk in group-housed sow systems. By explicitly acknowledging these limitations and methodological boundaries, the thesis aims to provide a balanced and transparent foundation for both scientific interpretation and the translation of research findings into meaningful welfare assessment and management decisions under practical production conditions.

7. Main conclusions

The overall aim of this thesis is to contribute with relevant knowledge about individual variation in behaviour and welfare in group-housed gilts and sows that is relevant for development of commercial pig production. Based on the combined findings of the studies included in this thesis, the following main conclusions can be drawn:

- Social mixing conditions during rearing influenced behavioural response patterns during social challenges and how social interactions translated into lesion outcomes later in life.
- Genetic background of gilts and sows influences behavioural expression, social response patterns, and lesion outcomes.
- Behavioural variation during social encounters was primarily expressed through differences in response strategies, including responses to unfamiliar conspecifics in standardised social tests across life stages.
- Lesion outcomes reflected exposure to social interactions and were, in some contexts, associated with behavioural response patterns.
- Lesions in group-housed gilts and sows are common in commercial herds and highly dependent on production stage and management conditions.
- Social behaviour and welfare-related outcomes in group-housed gilts and sows emerged from interactions between social environments and genetic background.
- The findings highlight differences between genetic lines and social environments, but none emerged as universally favourable.

7.1 Take-home message

In group-housed sow systems, what is ’sown’ early in life is not the absence of social conflict, but the behavioural strategies with which such conflict is met. Early-life social experience and genetic background did not determine whether gilts and sows engaged in social challenges but shaped how they responded across life stages. Lesion outcomes reflected cumulative exposure to social risk and were strongly context-dependent, underscoring that behavioural style and welfare outcome are not directly interchangeable. Thus, what is ultimately ’reaped’ in terms of welfare and sustainability emerges from the interaction between developmental experience, genotype and management context rather than from any single factor alone.

7.2 Practical implications for development of welfare assessment and management

Taken together, the findings of this thesis have several implications for the interpretation and management of welfare risk in commercial group-housed sow systems. Whilst not intended as prescriptive guidelines, the following points summarise key considerations for the development of welfare assessment, advisory work and management:

- Early social mixing during rearing influences behavioural flexibility and social response strategies later in life, rather than uniformly reducing aggression; expectations of early socialisation should therefore be placed on long-term coping capacity as opposed to immediate injury reduction.
- Behavioural indicators and lesion outcomes capture different dimensions of welfare risk and should be interpreted together rather than alone.
- Lesion prevalence reflects cumulative exposure to social challenges and may not be directly inferred from short-term behavioural responses observed during standardised tests.
- Late social mixing during rearing influenced behaviour-lesion relationships, indicating that rearing environment can shape cumulative injury risk through mechanisms not captured by short-term behavioural assessments, particularly around the transition into first parity.
- Environmental and management conditions shape whether behavioural flexibility translates into reduced injury risk, highlighting the importance of space, group stability and opportunities for avoidance.
- Genetic background modulates social response strategies rather than determining aggression per se, suggesting that breeding considerations should be integrated with management and housing conditions rather than viewed as single solutions.

- Welfare risk emerges from repeated social exposure over time, underscoring the importance of management decisions across the entire reproductive lifespan rather than at isolated time points.
- Differences between genetic lines and rearing environments were observed, but no specific line or social environment was universally favourable. The development of group-housed sow systems should therefore consider how opportunities for social experiences during gilt rearing align with both the management system in which the sows will later be housed and the social characteristics of the genetic lines used.

References

Ambruosi, S., De Angelis, F., Chou, J.-Y., & Goursot, C. (2024). Familiar versus unfamiliar: Revealing the complexity of sociability in pigs. *Applied Animal Behaviour Science*, *275*, 106248. https://doi.org/10.1016/j.applanim.2024.106248

Andersen, I. L., Bøe, K. E., & Kristiansen, A. L. (1999). The influence of different feeding arrangements and food type on competition at feeding in pregnant sows. *Applied Animal Behaviour Science*, *65*(2), 91–104. https://doi.org/10.1016/S0168-1591(99)00058-1

Andersson, E., Frössling, J., Engblom, L., Algers, B., & Gunnarsson, S. (2016). Impact of litter size on sow stayability in Swedish commercial piglet producing herds. *Acta Veterinaria Scandinavica*, *58*(1), 31. https://doi.org/10.1186/s13028-016-0213-8

Anil, L., Anil, S. S., Deen, J., Baidoo, S. K., & Walker, R. D. (2006). Effect of group size and structure on the welfare and performance of pregnant sows in pens with electronic sow feeders. *Canadian Journal of Veterinary Research*, *70*(2), 128–136.

Appleby, M. C., & Lawrence, A. B. (1987). Food restriction as a cause of stereotypic behaviour in tethered gilts. *Animal Science*, *45*(1), 103–110. https://doi.org/10.1017/S0003356100036680

Archer, J. (1988). *The Behavioural Biology of Aggression* (Vol. 4). Cambridge University Press.

Arey, D. S. (1999). Time course for the formation and disruption of social organisation in group-housed sows. *Applied Animal Behaviour Science*, *62*(2), 199–207. https://doi.org/10.1016/S0168-1591(98)00224-X

Arey, D. S., & Edwards, S. A. (1998). Factors influencing aggression between sows after mixing and the consequences for welfare and production. *Livestock Production Science*, *56*(1), 61–70. https://doi.org/10.1016/S0301-6226(98)00144-4

Barnett, J. L., Hemsworth, P. H., Cronin, G. M., Jongman, E. C., & Hutson, G. D. (2001). A review of the welfare issues for sows and piglets in relation to housing. *Australian Journal of Agricultural Research*, *52*(1), 1–28. https://doi.org/10.1071/AR00057

Barnett, J. L., Hemsworth, P. H., Newman, E. A., McCallum, T. H., & Winfield, C. G. (1989). The effect of design of tether and stall housing on some behavioural and physiological responses related to the welfare of pregnant pigs. *Applied Animal Behaviour Science*, *24*(1), 1–12. https://doi.org/10.1016/0168-1591(89)90120-2

Baxter, E. M., Lawrence, A. B., & Edwards, S. A. (2011). Alternative farrowing systems: Design criteria for farrowing systems based on the biological needs of sows and piglets. *Animal*, *5*(4), 580–600. https://doi.org/10.1017/S1751731110002272

Baxter, E. M., Moustsen, V. A., Boyle, L. A., & Edwards, S. A. (2025). 'End the cage age': Review of technical issues associated with the replacement of farrowing crates for sows and proposals for harmonized legislation. *Frontiers in Animal Science*, *6, 1598647.* https://doi.org/10.3389/fanim.2025.1598647

Bergsma, R., Kanis, E., Knol, E. F., & Bijma, P. (2008). The Contribution of Social Effects to Heritable Variation in Finishing Traits of Domestic Pigs (Sus scrofa). *Genetics*, *178*(3), 1559–1570. https://doi.org/10.1534/genetics.107.084236

Blackshaw, J. K., Blackshaw, A. W., Thomas, F. J., & Newman, F. W. (1994). Comparison of behaviour patterns of sows and litters in a farrowing crate and a farrowing pen. *Applied Animal Behaviour Science, Advances in Pig Behaviour Science*, *39*(3), 281–295. https://doi.org/10.1016/0168-1591(94)90163-5

Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., & Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology & Behavior, Stress and Welfare in Farm Animals*, *92*(3), 375–397. https://doi.org/10.1016/j.physbeh.2007.02.003

Boitani, L., Mattei, L., Nonis, D., & Corsi, F. (1994). Spatial and Activity Patterns of Wild Boars in Tuscany, Italy. *Journal of Mammalogy*, *75*(3), 600–612. https://doi.org/10.2307/1382507

Boonkum, W., Permthongchoochai, S., Chankitisakul, V., & Duangjinda, M. (2025). Genetic strategies for enhancing litter size and birth weight uniformity in piglets. *Frontiers in Veterinary Science*, *12,* 1512701 https://doi.org/10.3389/fvets.2025.1512701

Brajon, S., Ahloy-Dallaire, J., Devillers, N., & Guay, F. (2020). The Role of Genetic Selection on Agonistic Behavior and Welfare of Gestating Sows Housed in Large Semi-Static Groups. *Animals 2020, 10*(12), 2299. https://doi.org/10.3390/ANI10122299

Briffa, M., & Lane, S. M. (2017). The role of skill in animal contests: A neglected component of fighting ability. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1863). https://doi.org/10.1098/rspb.2017.1596

Broom, D. M. (1986). Indicators of poor welfare. *British Veterinary Journal*, *142*(6), 524–526. https://doi.org/10.1016/0007-1935(86)90109-0

Burfoot, A., Kay, R. M., & Corning, S. (1995). A scoring method to assess damage caused by aggression between sows after mixing. *Proceedings of the British Society of Animal Science*, *1995*, 196–196. https://doi.org/10.1017/S175275620059190X

Caliebe, A., Nebel, A., Makarewicz, C., Krawczak, M., & Krause-Kyora, B. (2017). Insights into early pig domestication provided by ancient DNA analysis. *Scientific Reports*, *7*(1), 44550. https://doi.org/10.1038/srep44550

Camerlink, I., Farish, M., D'eath, R. B., Arnott, G., & Turner, S. P. (2018). Long term benefits on social behaviour after early life socialization of piglets. *Animals*, *8*(11). https://doi.org/10.3390/ani8110192

Camerlink, I., Proßegger, C., Kubala, D., Galunder, K., & Rault, J. L. (2021). Keeping littermates together instead of social mixing benefits pig social behaviour and growth post-weaning. *Applied Animal Behaviour Science*, *235*. https://doi.org/10.1016/j.applanim.2021.105230

Camerlink, I., Turner, S. P., Bijma, P., & Bolhuis, J. E. (2013). Indirect Genetic Effects and Housing Conditions in Relation to Aggressive Behaviour in Pigs. *PLOS ONE*, *8*(6), e65136. https://doi.org/10.1371/journal.pone.0065136

Camerlink, I., Turner, S. P., Farish, M., & Arnott, G. (2015). Aggressiveness as a component of fighting ability in pigs using a game-theoretical framework. *Animal Behaviour*, *108*, 183–191. https://doi.org/10.1016/j.anbehav.2015.07.032

Camerlink, I., Turner, S. P., Farish, M., & Arnott, G. (2017). The influence of experience on contest assessment strategies. *Scientific Reports*, *7*(1). https://doi.org/10.1038/S41598-017-15144-8

Camerlink, I., Turner, S. P., Ursinus, W. W., Reimert, I., & Bolhuis, J. E. (2014). Aggression and Affiliation during Social Conflict in Pigs. *PLoS ONE*, *9*(11), e113502. https://doi.org/10.1371/journal.pone.0113502

Canario, L., Turner, S. P., Roehe, R., Lundeheim, N., D'Eath, R. B., Lawrence, A. B., Knol, E., Bergsma, R., & Rydhmer, L. (2012). Genetic associations between behavioral traits and direct-social effects of growth rate in pigs. *Journal of Animal Science*, *90*(13), 4706–4715. https://doi.org/10.2527/jas.2012-5392

Clouard, C., Foreau, A., Goumon, S., Tallet, C., Merlot, E., & Resmond, R. (2024). Evidence of stable preferential affiliative relationships in the domestic pig. *Animal Behaviour*, *213*, 95–105. https://doi.org/10.1016/j.anbehav.2024.04.009

Colditz, I. G., & Hine, B. C. (2016). Resilience in farm animals: Biology, management, breeding and implications for animal welfare. *Animal Production Science*, *56*(12), 1961–1983. https://doi.org/10.1071/AN15297

Collarini, E., Gioia, M., Cordoni, G., & Norscia, I. (2022). Does the Domestication Syndrome Apply to the Domestic Pig? Not Completely. *Animals*, *12*(18), 2458. https://doi.org/10.3390/ani12182458

Coppens, C. M., De Boer, S. F., & Koolhaas, J. M. (2010). Coping styles and behavioural flexibility: Towards underlying mechanisms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4021–4028. https://doi.org/10.1098/rstb.2010.0217

Dardaillon, M. (1988). Wild boar social groupings and their seasonal changes in the Camargue, southern France. *Zeitschrift Für Säugetierkunde : Im Auftrage Der Deutschen Gesellschaft Für Säugetierkunde e.V*, *53*, 22–30.

D'Eath, R. B. (2005). Socialising piglets before weaning improves social hierarchy formation when pigs are mixed post-weaning. *Applied Animal Behaviour Science*, *93*(3–4), 199–211. https://doi.org/10.1016/j.applanim.2004.11.019

D'Eath, R. B., & Turner, S. P. (2009). The Natural Behaviour of the Pig. In J. N. Marchant-Forde (Ed.), *The Welfare of Pigs* (pp. 13–45). Springer Netherlands. https://doi.org/10.1007/978-1-4020-8909-1_2

Desire, S., Calderón Díaz, J. A., Lewis, C. R. G., Roehe, R., & Turner, S. P. (2023). Genetic associations between human-directed behavior and intraspecific social aggression in growing pigs. *Journal of Animal Science*, *101*, skad070. https://doi.org/10.1093/jas/skad070

EFSA, Nielsen, S. S., Alvarez, J., Bicout, D. J., Calistri, P., Canali, E., Drewe, J. A., Garin-Bastuji, B., Gonzales Rojas, J. L., Schmidt, G., Herskin, M., Michel, V., Miranda Chueca, M. Á., Mosbach-Schulz, O., Padalino, B., Roberts, H. C., Stahl, K., Velarde, A., Viltrop, A., … Spoolder, H. (2022). Welfare of pigs on farm—Panel on Animal Health and Welfare (AHAW). *EFSA Journal*, *20*(8), e07421. https://doi.org/10.2903/j.efsa.2022.7421

Engblom, L., Eliasson-Selling, L., Lundeheim, N., Belák, K., Andersson, K., & Dalin, A.-M. (2008). Post mortem findings in sows and gilts euthanised or found dead in a large Swedish herd. *Acta Veterinaria Scandinavica*, *50*(1), 25. https://doi.org/10.1186/1751-0147-50-25

Engblom, L., Lundeheim, N., Dalin, A. M., & Andersson, K. (2007). Sow removal in Swedish commercial herds. *Livestock Science*, *106*(1), 76–86. https://doi.org/10.1016/J.LIVSCI.2006.07.002

Erdtmann, D., & Keuling, O. (2020). Behavioural patterns of free roaming wild boar in a spatiotemporal context. *PeerJ*, *8*, e10409. https://doi.org/10.7717/peerj.10409

European Citizens' Initiative. (2025). *End the Cage Age*. European Union. https://citizens-initiative.europa.eu/initiatives/details/2018/000004/end-cage-age_en

Fels, M., Schrey, L., Rauterberg, S., & Kemper, N. (2021). Early socialisation in group lactation system reduces post-weaning aggression in piglets. *Veterinary Record*, *189*(12), e830. https://doi.org/10.1002/vetr.830

Fraser, D. (2003). Assessing Animal Welfare at the Farm and Group Level: The Interplay of Science and Values. *Animal Welfare*, *12*(4), 433–443. https://doi.org/10.1017/S0962728600026038

Fraser, D., Kramer, D. L., Pajor, E. A., & Weary, D. M. (1995). Conflict and cooperation: Sociobiological principles and the behaviour of pigs. *Applied Animal Behaviour Science, International Society for Applied Ethology 1995*, *44*(2), 139–157. https://doi.org/10.1016/0168-1591(95)00610-5

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Friend, T. H., Knabe, D. A., & Tanksley, T. D. (1983). Behavior and performance of pigs grouped by three different methods at weaning. *Journal of Animal Science*, *57*(6), 1406–1411. https://doi.org/10.2527/jas1983.5761406x

Gabor, T. M., Hellgren, E. C., Van Den Bussche, R. A., & Silvy, N. J. (1999). Demography, sociospatial behaviour and genetics of feral pigs (Sus scrofa) in a semi-arid environment. *Journal of Zoology*, *247*(3), 311–322. https://doi.org/10.1111/j.1469-7998.1999.tb00994.x

Giuffra, E., Kijas, J. M., Amarger, V., Carlborg, O., Jeon, J. T., & Andersson, L. (2000). The origin of the domestic pig: Independent domestication and subsequent introgression. *Genetics*, *154*(4), 1785–1791. https://doi.org/10.1093/genetics/154.4.1785

Graves, H. B. (1984). Behavior and Ecology of Wild and Feral Swine (Sus Scrofa). *Journal of Animal Science*, *58* (2), 482–492. https://doi.org/10.2527/jas1984.582482x

Greenwood, E. C., Plush, K. J., van Wettere, W. H. E. J., & Hughes, P. E. (2014). Hierarchy formation in newly mixed, group housed sows and management strategies aimed at reducing its impact. *Applied Animal Behaviour Science*, *160*, 1–11. https://doi.org/10.1016/j.applanim.2014.09.011

Gustafsson, M., Jensen, P., de Jonge, F. H., Illmann, G., & Spinka, M. (1999). Maternal behaviour of domestic sows and crosses between domestic sows and wild boar. *Applied Animal Behaviour Science*, *65*(1), 29–42. https://doi.org/10.1016/S0168-1591(99)00048-9

Heinonen, M., Peltoniemi, O., & Valros, A. (2013). Impact of lameness and claw lesions in sows on welfare, health and production. *Livestock Science, Lameness and Claw Lesions in Sows, Cows and Small Ruminants*, *156*(1), 2–9. https://doi.org/10.1016/j.livsci.2013.06.002

Hemsworth, P., Mellor, D., Cronin, G., & Tilbrook, A. (2015). Scientific assessment of animal welfare. *New Zealand Veterinary Journal*, *63*(1), 24–30. https://doi.org/10.1080/00480169.2014.966167

Hessel, E. F., Reiners, K., & Van Den Weghe, H. F. A. (2006). Socializing piglets before weaning: Effects on behavior of lactating sows, pre- and postweaning behavior, and performance of piglets. *Journal of Animal Science*, *84*(10), 2847–2855. https://doi.org/10.2527/jas.2005-606

Hidås, L., Ehrenkrona, W., Reneby, A., & Eriksson, I. (2025). *Hållbarhet hos svenska suggor* (Slutrapport No. P263), https://doi.org/10.2527/jas1984.582482x, 1–30. Gård & Djurhälsan. https://www.gardochdjurhalsan.se/nationellt-ansvar/projekt/avslutade-projekt-gris/hallbarhet-hos-svenska-suggor/

Högberg, N., Skånberg, L., Guzhva, O., Westin, R., Sannö, A., Wallenbeck, A., & Rørvang, M. V. (2025). Do pigs like to brush? An observational study of pig brushing behaviour in a commercial production environment. *Frontiers in Animal Science*, *6*. https://doi.org/10.3389/fanim.2025.1712426

Horback, K. (2014). Nosing Around: Play in Pigs. *Animal Behavior and Cognition*, *2*(2), 186. https://doi.org/10.12966/abc.05.08.2014

Hoy, S., Bauer, J., Borberg, C., Chonsch, L., & Weirich, C. (2009). Investigations on dynamics of social rank of sows during several parities. *Applied Animal Behaviour Science*, *121*(2), 103–107. https://doi.org/10.1016/j.applanim.2009.09.003

Janczak, A. M., Pedersen, L. J., & Bakken, M. (2003). Aggression, fearfulness and coping styles in female pigs. *Applied Animal Behaviour Science*, *81*(1), 13–28. https://doi.org/10.1016/S0168-1591(02)00252-6

Jang, J.-C., & Oh, S.-H. (2022). Management factors affecting gestating sows' welfare in group housing systems—A review. *Animal Bioscience*, *35*(12), 1817–1826. https://doi.org/10.5713/ab.22.0289

Jensen, P. (1986). Observations on the maternal behaviour of free-ranging domestic pigs. *Applied Animal Behaviour Science*, *16*(2), 131–142. https://doi.org/10.1016/0168-1591(86)90105-X

Jensen, P. (2022). Behaviour of Pigs. In *The ethology of domestic animals* (Vol. 2022, pp. 159–172). CABI Publishing. https://www.cabidigitallibrary.org/doi/epdf/10.1079/9780851996028.0159

Jensen, P., & Redbo, I. (1987). Behaviour during nest leaving in free-ranging domestic pigs. *Applied Animal Behaviour Science*, *18*(3–4), 355–362. https://doi.org/10.1016/0168-1591(87)90229-2

Kaminski, G., Brandt, S., Baubet, E., & Baudoin, C. (2005). Life-history patterns in female wild boars (Sus scrofa): Mother–daughter postweaning associations. *Https://Doi.Org/10.1139/Z05-019*, *83*(3), 474–480. https://doi.org/10.1139/Z05-019

Kanaan, V. T., Lay, D. C., Richert, B. T., & Pajor, E. A. (2012). Increasing the Frequency of Co-Mingling Piglets During the Lactation Period Alters the Development of Social Behavior Before and After Weaning. *Journal of applied animal welfare science: JAAWS*, 15(2), 163–180. https://doi.org/10.1080/10888705.2012.658333

Kanis, E., De Greef, K. H., Hiemstra, A., & van Arendonk, J. a. M. (2005). Breeding for societally important traits in pigs. *Journal of Animal Science*, *83*(4), 948–957. https://doi.org/10.2527/2005.834948x

Kanitz, E., Tuchscherer, M., Otten, W., Tuchscherer, A., Zebunke, M., & Puppe, B. (2019). Coping Style of Pigs Is Associated With Different Behavioral, Neurobiological and Immune Responses to Stressful Challenges. *Frontiers in Behavioral Neuroscience*, *13*, 173. https://doi.org/10.3389/fnbeh.2019.00173

Ketchem, R., Rix, M., & Sharp, C. (2020). *What is going on with female death loss and culling?* National Hog Farmer. https://www.nationalhogfarmer.com/livestock-management/what-is-going-on-with-female-death-loss-and-culling-

Keuling, O., Stier, N., & Roth, M. (2008). How does hunting influence activity and spatial usage in wild boar Sus scrofa L.? *European Journal of Wildlife Research*, *54*(4), 729–737. https://doi.org/10.1007/s10344-008-0204-9

Ko, H. L., Chong, Q., Escribano, D., Camerlink, I., Manteca, X., & Llonch, P. (2020). Pre-weaning socialization and environmental enrichment affect life-long response to regrouping in commercially-reared pigs. *Applied Animal Behaviour Science*, *229*. https://doi.org/10.1016/j.applanim.2020.105044

Kongsted, H., & Krogh, M. A. (2025). Sow mortality in Danish herds – Differences between production systems, annual and seasonal trends and association to herd sizes. *Preventive Veterinary Medicine*, *244*, 106662. https://doi.org/10.1016/j.prevetmed.2025.106662

Krause, A., Puppe, B., & Langbein, J. (2017). Coping Style Modifies General and Affective Autonomic Reactions of Domestic Pigs in Different Behavioral Contexts. *Frontiers in Behavioral Neuroscience*, *11*. https://doi.org/10.3389/fnbeh.2017.00103

Kutzer, T., Bünger, B., Kjaer, J. B., & Schrader, L. (2009). Effects of early contact between non-littermate piglets and of the complexity of farrowing conditions on social behaviour and weight gain. *Applied Animal Behaviour Science*, *121*(1), 16–24. https://doi.org/10.1016/j.applanim.2009.08.004

Larson, G., Albarella, U., Dobney, K., & Rowley-Conwy, P. (2007). *Current views on Sus phylogeography and pig domestication as seen through modern mtDNA studies*, Pigs and Humans: 10,000 Years of Interaction. Oxford Academic, 30–41. https://doi.org/10.1093/oso/9780199207046.003.0010

Larson, G., Dobney, K., Albarella, U., Fang, M., Matisoo-Smith, E., Robins, J., Lowden, S., Finlayson, H., Brand, T., Willerslev, E., Rowley-Conwy, P., Andersson, L., & Cooper, A. (2005). Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science*, *307*(5715), 1618–1621. https://doi.org/10.1126/science.1106927

Lawrence, A. B., Vigors, B., & Sandøe, P. (2019). What Is so Positive about Positive Animal Welfare? — A Critical Review of the Literature. *Animals*, *9*(10), 783. https://doi.org/10.3390/ani9100783

Lee, V. E., Arnott, G., & Turner, S. P. (2022). Social behavior in farm animals: Applying fundamental theory to improve animal welfare. *Frontiers in Veterinary Science*, *9*, 932217. https://doi.org/10.3389/fvets.2022.932217

Li, C., & Gu, X. (2024). Oral stereotypic behaviors in farm animals and their causes. *Animal Research and One Health*, *2*(3), 337–351. https://doi.org/10.1002/aro2.48

Liu, X., Song, P., Yan, H., Zhang, L., Wang, L., Zhao, F., Gao, H., Hou, X., Shi, L., Li, B., & Wang, L. (2021). A Comparison of the Behavior, Physiology, and Offspring Resilience of Gestating Sows When Raised in a Group Housing System and Individual Stalls. *Animals*, *11*(7), 2076. https://doi.org/10.3390/ani11072076

Løvendahl, P., Damgaard, L. H., Nielsen, B. L., Thodberg, K., Su, G., & Rydhmer, L. (2005). Aggressive behaviour of sows at mixing and maternal behaviour are heritable and genetically correlated traits. *Livestock Production Science, 93(1),* 73–85. https://doi.org/10.1016/j.livprodsci.2004.11.008

Lucia, T., Dial, G. D., & Marsh, W. E. (2000). Lifetime reproductive and financial performance of female swine. *Journal of the American Veterinary Medical Association*, *216*(11), 1802–1809. https://doi.org/10.2460/javma.2000.216.1802

Lundeheim, N. *The rise and fall of Swedish pig breeding—Pros and cons with genes from abroad*. [Conference presentation]. XVIII Baltic Animal Breeding Conference, Lithuania, 30–31 May 2017.

Luttman, A. M., Lee, B., Siegford, J. M., Steibel, J. P., Raney, N. E., & Ernst, C. W. (2023). Characterizing resilience to weaning stress and its associations with behavioral differences in finishing gilts. *Applied Animal Behaviour Science*, *263*, 105940. https://doi.org/10.1016/j.applanim.2023.105940

Marchant-Forde, J. N. (2009). Aggression and mixing. In *The Welfare of Pigs.* (pp. 113-114 (Chapter 4.5.1.1)). Springer Science.

Marchant-Forde, J. N., & Marchant-Forde, R. M. (2005). Minimizing inter-pig aggression during mixing. *Pig News and Information*. *26*, 63–71.

Mauget, R. (1981). Behavioural and Reproductive Strategies in Wild Forms of Sus scrofa (European Wild Boar and Feral Pigs). In W. Sybesma (Ed.), *The Welfare of Pigs* (pp. 3–15). Springer Netherlands. https://doi.org/10.1007/978-94-011-9574-4_1

McGlone, J. J. (1985). A quantitative ethogram of aggressive and submissive behaviors in recently regrouped pigs. *Journal of Animal Science*, *61*(3), 559–565. https://doi.org/10.2527/jas1985.613556x

Mellor, D. (2012). Animal emotions, behaviour and the promotion of positive welfare states. *New Zealand Veterinary Journal*, *60*(1), 1–8. https://doi.org/10.1080/00480169.2011.619047

Minitab, LLC. (2022). *Minitab Statistical Software* (Version 21.3.1) [Computer software]. Minitab, LLC. https://www.minitab.com

Moeller, G. A., & Stalder, K. J. (2024). Sow longevity. In *Advances in Pig Welfare (Second Edition)*, 163–184. Woodhead Publishing. https://doi.org/10.1016/B978-0-323-85676-8.00001-8

Moore, A. S., Gonyou, H. W., & Ghent, A. W. (1993). Integration of newly introduced and resident sows following grouping. *Applied Animal Behaviour Science*, *38*(3), 257–267. https://doi.org/10.1016/0168-1591(93)90024-J

Morgan, T., Pluske, J., Miller, D., Collins, T., Barnes, A. L., Wemelsfelder, F., & Fleming, P. A. (2014). Socialising piglets in lactation positively affects their post-weaning behaviour. *Applied Animal Behaviour Science*, *158*, 23–33. https://doi.org/10.1016/j.applanim.2014.06.001

Murphy, E., Nordquist, R. E., & van der Staay, F. J. (2014). A review of behavioural methods to study emotion and mood in pigs, *Sus scrofa*. *Applied Animal Behaviour Science*, *159*, 9–28. https://doi.org/10.1016/j.applanim.2014.08.002

Nannoni, E., Aarnink, A. J. A., Vermeer, H. M., Reimert, I., Fels, M., & Bracke, M. B. M. (2020). Soiling of Pig Pens: A Review of Eliminative Behaviour. *Animals*, *10*(11), 2025. https://doi.org/10.3390/ani10112025

Newberry, R. C., Wood-Gush, D. G. M., & Hall, J. W. (1988). Playful behaviour of piglets. *Behavioural Processes*, *17*(3), 205–216. https://doi.org/10.1016/0376-6357(88)90004-6

Oldham, L., Arnott, G., Camerlink, I., Doeschl-Wilson, A., Farish, M., Wemelsfelder, F., & Turner, S. P. (2021). Once bitten, twice shy: Aggressive and defeated pigs begin agonistic encounters with more negative emotions. *Applied Animal Behaviour Science*, *244*, 105488. https://doi.org/10.1016/j.applanim.2021.105488

Oldham, L., Camerlink, I., Arnott, G., Doeschl-Wilson, A., Farish, M., & Turner, S. P. (2020). Winner–loser effects overrule aggressiveness during the early stages of contests between pigs. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-69664-x

O’Malley, C. I., Steibel, J. P., Bates, R. O., Ernst, C. W., & Siegford, J. M. (2022). The Social Life of Pigs: Changes in Affiliative and Agonistic Behaviors following Mixing. *Animals*, *12*(2), 206. https://doi.org/10.3390/ani12020206

Pajor, E. A. (2004). Sow housing: Science, behavior, and values. *Journal of the American Veterinary Medical Association, 226*(8), 1340–1344. https://doi.org/10.2460/javma.2005.226.1340

Pedersen, L. J. (2018). Overview of commercial pig production systems and their main welfare challenges. In *Advances in Pig Welfare* (pp. 3–25). Woodhead Publishing. https://doi.org/10.1016/B978-0-08-101012-9.00001-0

Petersen, H. V., Vestergaard, K., & Jensen, P. (1989). Integration of piglets into social groups of free-ranging domestic pigs. *Applied Animal Behaviour Science*, *23*(3), 223–236. https://doi.org/10.1016/0168-1591(89)90113-5

Podgórski, T., Baś, G., Jędrzejewska, B., Sönnichsen, L., Śnieżko, S., Jędrzejewski, W., & Okarma, H. (2013). Spatiotemporal behavioral plasticity of wild boar (Sus scrofa) under contrasting conditions of human pressure: Primeval forest and metropolitan area. *Journal of Mammalogy*, *94*(1), 109–119. https://doi.org/10.1644/12-MAMM-A-038.1

Podgórski, T., Lusseau, D., Scandura, M., Sönnichsen, L., & Jędrzejewska, B. (2014). Long-Lasting, Kin-Directed Female Interactions in a Spatially Structured Wild Boar Social Network. *PLOS ONE*, *9*(6), e99875. https://doi.org/10.1371/JOURNAL.PONE.0099875

Price, E. (1984). Behavioral Aspects of Animal Domestication. *The Quarterly Review of Biology, 59*(1), 1–32. https://doi.org/10.1086/413673

R Core Team. (2024). *R: A Language and Environment for Statistical Computing* [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Rault, J.-L., Hintze, S., Camerlink, I., & Yee, J. R. (2020). Positive Welfare and the Like: Distinct Views and a Proposed Framework. *Frontiers in Veterinary Science*, *7*. https://doi.org/10.3389/fvets.2020.00370

Rault, J.-L., Sandøe, P., Sonntag, Q., & Stuardo, L. (2022). Positive Animal Welfare: Bridging the Gap or Raising Inequalities Worldwide? *Frontiers in Animal Science*, *3*. 825379. https://doi.org/10.3389/fanim.2022.825379

Reimert, I., Bolhuis, J. E., Kemp, B., & Rodenburg, T. B. (2014). Social support in pigs with different coping styles. *Physiology & Behavior*, *129*, 221–229. https://doi.org/10.1016/j.physbeh.2014.02.059

Robertson, J. B., Laird, R., Hall, J. K. S., Forsyth, R. J., Thomson, J. M., & Walker-Love, J. (1966). A comparison of two indoor farrowing systems for sows. *Animal Science*, *8*(2), 171–178. https://doi.org/10.1017/S0003356100034553

Rundgren, M., & Löfquist, I. (1989). Effects on performance and behaviour of mixing 20-kg pigs fed individually. *Animal Science*, *49*(2), 311–315. https://doi.org/10.1017/S0003356100032451

Salazar, L. C., Ko, H. L., Yang, C. H., Llonch, L., Manteca, X., Camerlink, I., & Llonch, P. (2018). Early socialisation as a strategy to increase piglets' social skills in intensive farming conditions. *Applied Animal Behaviour Science*, *206*, 25–31. https://doi.org/10.1016/j.applanim.2018.05.033

SAS Institute Inc. (2013). *SAS software* (Version 9.4) [Computer software]. SAS Institute Inc.

Schley, L., & Roper, T. J. (2003). Diet of wild boar Sus scrofa in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review*, *33*(1), 43–56. https://doi.org/10.1046/j.1365-2907.2003.00010.x

Schuck-Paim, C., & Alonso, W. J. (2022). Productivity of mother pigs is lower, and mortality greater, in countries that still confine them in gestation crates. *F1000Research*, *11*, 564. https://doi.org/10.12688/f1000research.122*042.2*

Spinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian Play: Training for the Unexpected. *The Quarterly review of biology, 76*(2), 141–168. https://doi.org/10.1086/393866

Spoolder, H. A. M., Geudeke, M. J., Van der Peet-Schwering, C. M. C., & Soede, N. M. (2009). Group housing of sows in early pregnancy: A review of success and risk factors. *Livestock Science*, *125*(1), 1–14. https://doi.org/10.1016/j.livsci.2009.03.009

Spoolder, H. A. M., & Vermeer, H. M. (2015). Gestation group housing of sows. In *The gestating and lactating sow* (pp. 47–71). Wageningen Academic. https://doi.org/10.3920/9789086868032_004

Stalder, K. J., Lacy, R. C., Cross, T. L., Conatser, G. E., & Darroch, C. S. (2000). Net Present Value Analysis of Sow Longevity and the Economic Sensitivity of Net Present Value to Changes in Production, Market Price, Feed Cost, and Replacement Gilt Costs in a Farrow-to-Finish Operation. *The Professional Animal Scientist*, *16*(1), 33–40. https://doi.org/10.15232/S1080-7446(15)31658-2

Stalder, K., Lacy, C., Cross, T., & Conatser, G. (2003). Financial impact of average parity of culled females in a breed-to-wean swine operation using replacement gilt net present value analysis. *Journal of Swine Health and Production*, *11*(2), 69–74. https://doi.org/10.54846/jshap/357

Steinerova, K. (2025). *The Role of Play Behaviour to Enhance Pig Welfare and Resilience and its Implications for the Swine Industry*. Diss. University of Saskatchewan. https://hdl.handle.net/10388/16736

Stolba, A., & Wood-Gush, D. G. (1984). The identification of behavioural key features and their incorporation into a housing design for pigs. *Annales de recherches veterinaires. Annals of veterinary research*, *15*(2), 287–299.

Stolba, A., & Wood-Gush, D. G. M. (1989). The behaviour of pigs in a semi-natural environment. *Animal Science*, *48*(2), 419–425. https://doi.org/10.1017/S000335610004041l

Tönepöhl, B., Appel, A. K., Voß, B., König von Borstel, U., & Gauly, M. (2013). Interaction between sows' aggressiveness post mixing and skin lesions recorded several weeks later. *Applied Animal Behaviour Science*, *144*(3–4), 108–115. https://doi.org/10.1016/j.applanim.2013.01.004

Turner, S. P. (2011). Breeding against harmful social behaviours in pigs and chickens: State of the art and the way forward. *Applied Animal Behaviour Science*, *134*(1), 1–9. https://doi.org/10.1016/j.applanim.2011.06.001

Turner, S. P., Camerlink, I., Baxter, E. M., D'eath, R. B., Desire, S., & Roehe, R. (2024). Breeding for pig welfare: Opportunities and challenges. In *Advances in Pig Welfare* (pp. 429–447). Woodhead Publishing. https://doi.org/10.1016/B978-0-323-85676-8.00003-1

Turner, S. P., D'Eath, R. B., Roehe, R., & Lawrence, A. B. (2010). Selection against aggressiveness in pigs at re-grouping: Practical application and implications for long-term behavioural patterns. *Animal Welfare*, *19*(1), 123–132. https://doi.org/10.1017/S0962728600002323

Turner, S. P., & Edwards, S. A. (2004). Housing immature domestic pigs in large social groups: Implications for social organisation in a hierarchical society. *Applied Animal Behaviour Science*, *87*(3), 239–253. https://doi.org/10.1016/j.applanim.2004.01.010

Turner, S. P., Farnworth, M. J., White, I. M. S., Brotherstone, S., Mendl, M., Knap, P., Penny, P., & Lawrence, A. B. (2006). The accumulation of skin lesions and their use as a predictor of individual aggressiveness in pigs. *Applied Animal Behaviour Science*, *96*(3–4), 245–259. https://doi.org/10.1016/j.applanim.2005.06.009

Turner, S. P., Nevison, I. M., Desire, S., Camerlink, I., Roehe, R., Ison, S. H., Farish, M., Jack, M. C., & D'Eath, R. B. (2017). Aggressive behaviour at regrouping is a poor predictor of chronic aggression in stable social groups. *Applied Animal Behaviour Science*, *191*, 98–106. https://doi.org/10.1016/j.applanim.2017.02.002

Turner, S. P., Roehe, R., D'Eath, R. B., Ison, S. H., Farish, M., Jack, M. C., Lundeheim, N., Rydhmer, L., & Lawrence, A. B. (2009). Genetic validation of postmixing skin injuries in pigs as an indicator of aggressiveness and the relationship with injuries under more stable social conditions1. *Journal of Animal Science*, *87*(10), 3076–3082. https://doi.org/10.2527/jas.2008-1558

Turner, S. P., Roehe, R., Mekkawy, W., Farnworth, M. J., Knap, P. W., & Lawrence, A. B. (2008). Bayesian Analysis of Genetic Associations of Skin Lesions and Behavioural Traits to Identify Genetic Components of Individual Aggressiveness in Pigs. *Behavior Genetics*, *38*(1), 67–75. https://doi.org/10.1007/s10519-007-9171-2

Turner, S. P., Weller, J. E., Camerlink, I., Arnott, G., Choi, T., Doeschl-Wilson, A., Farish, M., & Foister, S. (2020). Play fighting social networks do not predict injuries from later aggression. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-72477-7

Vaishnav, S., Saini, T., Firdous Ahmad, S., Kumar Gaur, G., Mehrotra, A., & Chauhan, A. (2025). Breeding management in commercial pig farms. In *Commercial Pig Farming* (pp. 29–46). Academic Press. https://doi.org/10.1016/B978-0-443-23769-0.00003-8

Van Kerschaver, C., Turpin, D., Michiels, J., & Pluske, J. (2023). Reducing Weaning Stress in Piglets by Pre-Weaning Socialization and Gradual Separation from the Sow: A Review. *Animals*, *13*(10), 1644. https://doi.org/10.3390/ani13101644

Van Putten, G., & Buré, R. G. (1997). Preparing gilts for group housing by increasing their social skills. *Applied Animal Behaviour Science*. https://doi.org/10.1016/S0168-1591(97)00063-4

Varela, S. A. M., Teles, M. C., & Oliveira, R. F. (2020). The correlated evolution of social competence and social cognition. *Functional Ecology*, *34*(2), 332–343. https://doi.org/10.1111/1365-2435.13416

Verdon, M., Hansen, C. F., Rault, J. L., Jongman, E., Hansen, L. U., Plush, K., & Hemsworth, P. H. (2015). Effects of group housing on sow welfare: A review. *Journal of Animal Science*, *93*(5), 1999–2017. https://doi.org/10.2527/jas.2014-8742

Verdon, M., Morrison, R. S., & Rault, J.-L. (2020). The welfare and productivity of sows and piglets in group lactation from 7, 10, or 14 d postpartum. *Journal of Animal Science*, *98*(3), skaa037. https://doi.org/10.1093/jas/skaa037

Wallenbeck, A., Carlzen, H., Karlsson, E., Hannius, L. M., & Westin, R. (2024). *Unplanned culling and mortality in group housed sows – effects of housing and management*. 9th International Conference on the Welfare Assessment of Animals at Farm Level, 30-31 September 2024, Florence Italy. https://res.slu.se/id/publ/132939

Wattanakul, W., Stewart, A. H., Edwards, S. A., & English, P. R. (1997). Effects of grouping piglets and changing sow location on suckling behaviour and performance. *Applied Animal Behaviour Science*, *55*(1–2), 21–35. https://doi.org/10.1016/S0168-1591(97)00020-8

Welfare Quality® (2009). Welfare Quality® Assessment protocol for pigs (sows and piglets, growing and finishing pigs) Welfare Quality® Consortium, Lelystad, The Netherlands

Weller, J. E., Camerlink, I., Turner, S. P., Farish, M., & Arnott, G. (2019). Playful pigs: Early life play-fighting experience influences later life contest dynamics. *Animal Behaviour*, *158*, 269–279. https://doi.org/10.1016/j.anbehav.2019.09.019

Weller, J. E., Turner, S. P., Futro, A., Donbavand, J., Brims, M., & Arnott, G. (2020). The influence of early life socialisation on cognition in the domestic pig (Sus scrofa domestica). *Scientific Reports*, *10*(1), 19077. https://doi.org/10.1038/s41598-020-76110-5

Wen, C., van Dixhoorn, I., Schokker, D., Woelders, H., Stockhofe-Zurwieden, N., Rebel, J. M. J., & Smidt, H. (2021). Environmentally enriched housing conditions affect pig welfare, immune system and gut microbiota in early life. *Animal Microbiome*, *3*, 52. https://doi.org/10.1186/s42523-021-00115-2

Zurbrigg, K., & Blackwell, T. (2006). Injuries, lameness, and cleanliness of sows in four group-housing gestation facilities in Ontario. *Journal of Swine Health and Production*, *14*(4), 202–206.

Popular science summary

When unfamiliar sows are mixed into groups, they often fight. These conflicts are part of how pigs establish social hierarchies. In commercial production systems, however, aggression can lead to stress and injuries. Injuries not only affect the individual animal's well-being; they can also reduce the ability to function in a group over time, which may ultimately lead to removal from the herd. As group housing of sows is standard practice in Sweden and becoming increasingly common in other countries, understanding how female pigs cope with social challenges is essential for improving animal welfare.

Pigs are highly social animals. Under natural conditions, young females (gilts) grow up in socially structured groups that include several related females and their offspring, where they gradually develop social skills through repeated interactions. In modern pig production, however, early life looks different. Piglets are typically raised with their littermates, and major social challenges occur later, for example at weaning or when animals are regrouped. Furthermore, breeding programmes have selected animals in housing systems with few opportunities for social interactions, which may have shaped behavioural tendencies across generations. This raises an important question: how do genetic background and social experiences influence how pigs handle social conflict?

In this thesis, gilts from two genetic lines were followed from birth, through their first parity until immediately after weaning of the first litter. Their early social environment was manipulated, allowing some piglets to interact with neighbouring litters whilst others were raised within only their own litter. Later during rearing, some gilts were regrouped with unfamiliar animals, whilst others remained in stable groups. By following the same individuals across life stages, it was possible to study how behaviour develops over time and how early experiences are expressed later in life.

Differences were visible already during early rearing. Piglets with access to neighbouring litters showed more stable behavioural patterns around weaning, whereas those raised within their own litter displayed clearer behavioural shifts during the weaning transition. Genetic background was also linked to differences in how piglets used their environment and how they reacted to social interactions. These findings indicate that behavioural differences are shaped early in life, influenced by both genetic and social effects.

As the gilts matured, their responses to unfamiliar individuals were studied in controlled social encounters. At five and twenty weeks of age, differences between genetic lines were predominantly reflected in how much the animals explored their surroundings and how close they stayed to the other gilt in the test, rather than clear differences in aggression levels. Early social mixing was associated with a higher likelihood of play behaviour at twenty weeks, suggesting that early experiences may influence aspects of social development beyond aggression alone.

Clearer differences between genetic lines emerged when the females became first-parity sows and were confronted with an unfamiliar older sow. At this stage, Swedish Yorkshire sows were more likely to initiate damaging and warning behaviours and to respond forcefully when challenged compared to their Dutch Yorkshire counterparts. This also meant that they received more skin lesions during the encounter. These differences were therefore not only expressed in behaviour, but also in the physical consequences of social conflict.

Early and later social experiences influenced behaviour in more subtle ways. Sows that had experienced early mixing were more likely to show affiliative behaviour and were more often observed to not react when approached. Neither early nor later social mixing directly increased or decreased the overall number of lesions. Instead, social experience affected how behaviour and injuries were linked. In other words, early and later environments shaped how animals handled social challenges, even if they did not simply make animals more or less aggressive.

To place these experimental findings in a broader context, welfare indicators were assessed in Swedish commercial group-housed herds. Skin lesions were common, with around nine out of ten animals possessing at least one lesion. Lesion levels varied between animals, production stages and herds, and were influenced by factors such as group size, time since mixing and housing design. These results illustrate that injuries in group-housed systems are dependent on production stage and management conditions and cannot be understood without considering management and social conditions.

Taken together, this thesis shows that social behaviour and welfare-related outcomes develop across an animal's life. How a sow behaves in a conflict situation and the extent of her injuries are not only influenced by her genetic background, but also on the social experiences she has accumulated over time. No single factor alone determines how an individual copes in a group. Welfare in group housing therefore cannot be improved through isolated changes alone; it requires understanding the interaction between animals, their social environment and the systems in which they are kept.

Ultimately, improving welfare among sows in commercial production is not only about reducing injuries. It is about providing sows with the best possible foundation and support to manage the social challenges they encounter in modern production systems. Meaningful progress depends on aligning animals, management and environments, and acknowledging that pigs are socially complex individuals that live within equally complex production systems.

Populärvetenskaplig sammanfattning

När okända suggor blandas i nya grupper uppstår ofta slagsmål. Dessa konflikter är en naturlig del av hur grisar etablerar social rangordning. I kommersiella produktionssystem kan dock aggression leda till skador, stress och att djur tas ur produktion i förtid. Skador påverkar inte bara den enskilda suggans välbefinnande, utan kan också försämra hennes förmåga att fungera i en grupp över tid. Eftersom grupphållning av suggor sedan länge är standard i Sverige och blir allt vanligare även i andra länder är det viktigt att förstå hur gyltor och unga suggor hanterar sociala utmaningar för att kunna förbättra djurvälfärden.

Grisar är sociala djur. Under naturliga förhållanden växer unga hondjur upp i socialt strukturerade grupper med flera besläktade suggor i olika åldrar och deras avkommor, där de gradvis utvecklar sociala färdigheter genom upprepade interaktioner. I modern grisproduktion ser dock den tidiga miljön annorlunda ut. Smågrisar växer vanligtvis upp enbart med sina kullsyskon, och sociala utmaningar uppstår i stället senare, till exempel vid avvänjning eller omgruppering. Samtidigt har avelsurvalet skett i system med få möjligheter till sociala interaktioner, vilket kan ha påverkat beteendemässiga egenskaper över generationer. Detta väcker en central fråga: hur påverkar genetisk bakgrund och sociala erfarenheter hur grisar hanterar sociala konflikter?

I den här avhandlingen följdes gyltor från två avelslinjer från födsel till första grisningen och tiden direkt efter avvänjning av första kullen. Deras tidiga sociala miljö varierade, så att vissa smågrisar fick möjlighet att interagera med grannkullar genom ett hål mellan boxarna, medan andra hölls enbart med sin egen kull. Senare under uppfödningen omgrupperades en del gyltor med okända djur, medan andra fick gå kvar i stabila grupper. Genom att följa samma individer över flera livsstadier kunde beteendets utveckling studeras över tid och tidiga erfarenheter relateras till beteenden senare i livet.

Redan under den tidiga uppväxten kunde skillnader observeras. Gyltor som haft tillgång till grannkullar uppvisade mer stabila beteendemönster kring avvänjningen, medan de som vuxit upp enbart inom den egna kullen visade större förändringar i beteende i samband med avvänjningen. Även genetisk bakgrund var kopplad till skillnader i hur smågrisarna använde boxen och hur de reagerade på sociala interaktioner. Resultaten visar att beteendemönster formas tidigt i livet genom både genetiska och sociala faktorer.

När gyltorna blev äldre studerades deras reaktioner i kontrollerade möten med okända gyltor. Vid fem och tjugo veckors ålder visade de två genetiska linjerna skillnader i utforskande beteende och hur nära de höll sig till den andra gyltan i testet, snarare än i tydliga skillnader i aggressivitet. Tidig social blandning var vid tjugo veckors ålder kopplad till en högre förekomst av lekbeteende, vilket tyder på att tidiga erfarenheter kan påverka social utveckling på fler sätt än enbart genom aggression.

Tydligare skillnader mellan de genetiska linjerna framträdde när gyltorna blivit äldre och avvants från sin första egna kull. Här mötte de nu unga suggorna en äldre, okänd sugga i ett standardiserat test. Vid detta tillfälle var suggor av linjen Swedish Yorkshire mer benägna att initiera skadande och varningsbeteenden och att svara kraftfullt när de utmanades. Detta innebar också att de fick fler hudskador under mötet. Skillnaderna mellan linjerna kom alltså till uttryck inte bara i beteendet, utan även i de fysiska konsekvenserna av den sociala konflikten. Tidiga och senare sociala erfarenheter påverkade beteendet på mer subtila sätt. Suggor som haft möjlighet till tidig social blandning visade oftare affiliativa beteenden och reagerade i större utsträckning inte alls när den äldre suggan sökte kontakt. Varken tidig eller sen social blandning påverkade det totala antalet skador, men de påverkade hur beteenden och skador hängde samman. Med andra ord formade sociala erfarenheter hur djuren hanterade sociala utmaningar, även om de inte enkelt kunde beskrivas som mer eller mindre aggressiva.

För att sätta de experimentella resultaten i ett bredare sammanhang analyserades även djurbaserade välfärdsindikatorer i svenska kommersiella besättningar med grupphållna gyltor och suggor. Hudskador var vanliga, omkring nio av tio djur hade minst en skada. Skadenivåerna varierade mellan individer, produktionsstadier och besättningar och påverkades bland annat av gruppstorlek, tid sedan omgruppering och inhysningssystem. Resultaten visar att skador i grupphållna system är beroende av sammanhang och inte kan förstås utan att ta hänsyn till hur de hålls och sköts samt de sociala förhållandena som djuren upplevt.

Sammantaget visar avhandlingen att socialt beteende utvecklas över tid och att sociala interaktioner kan få konsekvenser för sårförekomst senare i livet. Hur en sugga beter sig i en konfliktsituation och hur mycket hon skadas påverkas av hennes genetiska bakgrund och av de sociala erfarenheter hon samlat på sig över tid. Ingen enskild faktor avgör hur en individ fungerar i en grupp. För att förbättra välfärden i grupphållning krävs därför en förståelse för samspelet mellan djurens egenskaper, deras sociala miljö och de produktionssystem de hålls i.

I slutändan handlar förbättrad välfärd hos suggor inte enbart om att minska antalet skador. Det handlar om att skapa förutsättningar som ger suggor möjlighet att hantera de sociala utmaningar de möter i moderna produktionssystem. Varaktiga förbättringar förutsätter att djur, management och miljö samspelar, och att man tar hänsyn till att grisar är socialt komplexa djur som lever i produktionssystem som är komplexa i sig själva.

Acknowledgements

This thesis marks the end of a journey that many people have contributed to along the way.

First and foremost, I would like to thank my supervisory team. Your guidance, support and patience have shaped both this project and me as a researcher.

To Anna Wallenbeck, my main supervisor**.**

You have been there since before this PhD was even officially a PhD. Thank you for letting me fully embrace my pig interest already as a research assistant, and for never questioning that it was a perfectly reasonable life choice. Thank you for your seemingly endless patience in explaining statistics. Repeatedly. In different ways. Until I (quietly) started to think it was actually… a little bit fun. You have been a constant driving force, and you have never shown even the slightest sign of losing faith in me, not even when models refused to converge or when I briefly did. But beyond the science, you have also been a steady source of support, perspective and encouragement. Knowing that you were there, both professionally and personally, has meant more than I can properly put into words. You are an exceptional supervisor, scientist and an even greater role model.

I have also been fortunate to work with wonderful co-supervisors who each contributed in their own way:

Linda, thank you for your sharp insights and your remarkable ability to see new layers in even the most familiar topics. You turn questions into small intellectual adventures, sometimes unexpected, always worthwhile. You always made time, even when your schedule was clearly full and that truly meant a lot to me.

Daiana, thank you for your warmth, thoughtful reflections and your ability to step into a discussion and gently make it better. You bring perspective and balance and I truly miss our fika breaks, an underrated but highly effective method for academic problem-solving.

Claes, thank you for being a steady and genuinely kind presence throughout this process. You always asked how I was doing… and meant it. Your thoughtful input has been perfectly balanced with fika conversations about Star Wars and your impressive talent for collecting… well, almost anything.

Rebecka, thank you for being a central part of Study II, for the farm visits and the invaluable reality checks. You showed me that while spreadsheets are useful, pigs rarely read them, and that research makes far more sense when grounded in reality.

I would also like to acknowledge the financial support that made this work possible. Both Study I and Study II were funded by the *Swedish Research Council for Sustainable Development* (**Formas**). I am also grateful to the *Royal Swedish Academy of Agriculture and Forestry* (**KSLA**) and *SLU GS-VMAS Mobility Support programme* for travel grants that enabled participation in international conferences and doctoral courses.

A very special thank you to the pig unit at Lövsta and especially to **Elin, Lisa, Ulrika, Christina, Jonna, Ida** & **Ulla**. While the experimental design lived on paper, the reality of it lived with you, and you handled it with patience, flexibility and remarkably few raised eyebrows. The experiments would have been far more complicated, and significantly less enjoyable, without you. Whether it was helping with practical arrangements, adjusting routines or simply saying "we'll sort it out," you made things work. The lunch breaks, fika moments and everyday conversations in the pig stable turned a sometimes demanding project into something much lighter.

A warm thank you also to the veterinarians who accompanied me on farm visits during Study II, **Helena, Josefine, Melina, Anna** and **Fredrik**. Thank you for wholeheartedly accepting that you would have a slightly confused PhD student tagging along. You always took the time to explain how you reasoned, what you observed and why you made the decisions you did. You generously invited me into your professional world, shared your perspectives on veterinary practice and sparked more research ideas than I could properly keep track of. I suspect our paths will cross again.

When I began my PhD, I belonged to HMH, a department that gave me my first academic home. Through the later merger with THV, that home expanded into an even larger and livelier community. I have been incredibly fortunate to be surrounded by **colleagues** who make lunches, fika breaks and everyday academic life far more enjoyable than it has any right to be. Mentioning everyone by name would be impossible, but please know how much I appreciate you all, and I am genuinely proud to be part of this community.

A special thank you to the PhD community, particularly those doctoral colleagues at HMH who were there when I began my journey as a slightly bewildered PhD student. **Lina, Sofia, Viktor, Per, Lena, Elin** and others, thank you for setting the tone, answering questions and proving that the finish line was, in fact, reachable. Some of you have since moved on from SLU, some I am fortunate to still call colleagues, and others I hope our paths will cross again in the future

I have been lucky to be part of several doctoral groups throughout my PhD. Within that extended doctoral community (naming everyone would require another thesis) were: **Svea, Claire, Markos, Leonie, Ida, Pontus, Jossan** (office buddy and fellow survivor of pig smells), **Johan, My, Vilma, Elin**, **Lea, Adrien, Lise, Kirste, Qasim, Melania, Valeriia, Renaud, Erika, Ulla, Patience, Adnan** and **many more**, some of you recently across the finish line, others progressing impressively toward it. Thank you for the laughter, the perspective and the reassuring realisation that uncertainty is a shared condition in academia.

I have inevitably left many of you **unnamed**, not from lack of gratitude, but from lack of pages. This thesis carries far more fika conversations than formal citations.

To **Lisa** and **Torun**, what began as innocent work friendships evolved into something far more dangerous (in the best possible way). Having friends who understand academia, its absurdities, pressures and its oddly satisfying breakthroughs, is invaluable. Having friends who understand everything beyond it is even more so. You have stood by me through absolutely everything these past years. There are few people as genuinely good as you, and none quite like you. I am very much looking forward to many more years of shared chaos, questionable decisions and a very solid friendship.

To friends outside academia: **Karin L, Lollo, Lotta, Clara, Emelie B, Karin B, Fredrik, Malin, Adam, Marcus, Emma, Katta, Astrid, Sara, Emelie A, Christoffer, Mesch** and **others**, thank you for asking "How is the pig research going?" year after year. You may not always have fully understood the answer (to be fair, sometimes neither did I), but you listened anyway. You reminded me that there is a world beyond seminars and statistical models. Your questions, often refreshingly free from academic jargon, were sometimes exactly the right ones. You kept me grounded, laughing and focused on things that matter far beyond a thesis.

To my family:

To my father, **Per**, you have been there from the very beginning, long before pigs, PhDs or academic ambitions were even a thought. Through every phase of life, you have been calm, reliable and ready to step in without hesitation. You have discussed pigs with impressive dedication over the years, despite never claiming any expertise, and followed this journey as if it were the most natural thing in the world. Thank you for being my hero (no cape required). After all, there is a reason you are called “Põssa”.

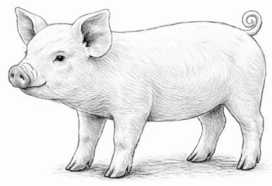
To my mother, **Anu**, who is not here to see this finished. Your influence runs quietly through everything I do. I wish you could have held this book in your hands.

To the animals who shaped me long before academia did, **Nurre** and **Cessi**, thank you for making me want to work with animals in the first place. And to **Akila, Lumi** and **Naya**, for daily reminders that fresh air, muddy paws and uncomplicated loyalty are sometimes better than any publication.

To my husband, **Daniel**, for sharing life with someone who occasionally talks more about pigs than people, and who has probably brought home more pig smell than anyone should reasonably have to endure. Thank you for your balance, humour and perspective, and for grounding me when I drift too far into overthinking. You have been carrying more than your share, more than once. I am very glad we are doing life together. Ma armastan sind. 💕

To **Leia**, you arrived in the middle of this process and quietly rearranged all priorities. You reminded me that not everything that is important can be measured, modelled or controlled, and that some things are infinitely more important than any result section. Minu armas Leilei. 💕

And finally, to all **pigs**, from the largest sows to the smallest piglets. You may not read this, but I hope the work behind it makes your lives, in some small way, better. I will keep trying.



ACTA AGRICULTURAE SCANDINAVICA, SECTION A — ANIMAL SCIENCE
2023, VOL. 72, NOS. 3–4, 135–148
https://doi.org/10.1080/09064702.2023.2245416

Taylor & Francis
Taylor & Francis Group

Effects of early social mixing and genetic line on female piglet activity, pen location and social interactions pre- and post-weaning under Swedish commercial pig production conditions

Linda Marie Backeman Hannius [a], Linda Keeling [a], Patricia Ask-Gullstrand [b], Else Verbeek [a] and Anna Wallenbeck [a]

[a]Department of Animal Environment and Health, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden; [b]Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden

ABSTRACT
This study investigated activity, preferred pen location and social interactions in female piglets (0–10 weeks of age, $N = 98$) intended for breeding. Piglets were housed in pens where the sow and the piglets were loose-housed without (CP) or with access to the neighbouring pen week 2–5 (AP). Female piglets of two genetic lines (Dutch and Swedish Yorkshire (DY, SY)) from 26 litters were selected within 24 h after birth. DY piglets in the AP treatment spent more time in the neighbouring pen than SY (24.0% vs 19.0%), while AP piglets of both genetic lines spent less time lying down before weaning than CP. At weaning, CP piglets increased their time in the piglet corner and spent less time lying. SY piglets were less responsive to social interactions. The results confirm previous findings on favourable effects of early social mixing on piglets' behavioural responses to weaning also when sows are individually loose-housed.

ARTICLE HISTORY
Received 6 January 2023
Accepted 2 August 2023

KEYWORDS
Piglet; female; social environment; co-mingling; genetic dam line; social behaviour; socialisation; general behaviour; animal welfare; early life

Introduction

As pigs are social animals, European Union (EU) regulations require group housing of pigs, with the exception of sows around farrowing and adult boars. However, mixing unfamiliar pigs often results in aggression, which can lead to injury, suffering and social stress, with negative effects on health and productivity (e.g. Arey & Edwards, 1998; Greenwood et al., 2014; Peden et al., 2018).

Piglets start to form relationships and establish a social hierarchy within the litter only a few hours after birth (Graves, 1984). Under feral and free-range conditions, piglets are involved in social interactions with unfamiliar piglets from other litters and older conspecifics of different ages in the maternal group of their mother from the first 1–2 weeks after birth (Jensen, 1986; Petersen et al., 1989; Wechsler, 1996). In modern pig production, the first mixing of unfamiliar pigs commonly occurs much later, after weaning, which usually occurs at around four to 5 weeks of age. After birth and survival during the first week in life, weaning is the next major challenge for piglets in modern pig production, with long-term effects on pig welfare and production, illustrated by stress responses altering behaviour, impaired performance including growth lag and gastrointestinal tract disorders leading to diarrhoea (e.g. Blavi et al., 2021; Van Kerschaver et al., 2023).

With the change in EU regulations (EU Directive on minimum standards for the protection of pigs (2008/120/EC)) requiring group housing instead of individual stalls for sows during gestation, there has been an increased focus among pig producers, authorities and researchers on management of group-housed sows, including prevention of negative effects such as injurious aggressive behaviour (Greenwood et al., 2014; Peden et al., 2018). Methods to reduce such unwanted damaging behaviours in commercial pig production have been sought, initially focusing on space allowance and group size, but in later years also on genetic selection, nutritional aspects, early-life socialisation (also termed co-mingling) and use of pheromones (e.g. Greenwood et al., 2014; Peden et al., 2018; Ko et al., 2020; Rydhmer, 2020). Early-life socialisation is reported to have long-term benefits such as fewer aggressive interactions when meeting unfamiliar pigs later in life

CONTACT Backeman Hannius linda.marie.hannius@slu.se Department of Animal Environment and Health, Swedish University of Agricultural Sciences (SLU), P.O. Box 7068, SE-750 07 Uppsala, Sweden

(e.g. Salazar et al., 2018; Ko et al., 2020). Methods shown to reduce unwanted damaging behaviours in group-housed adult sows are likely also to affect the sows early in life, including the period pre- and post-weaning (Van Kerschaver et al., 2023). For example, a combination of pre-weaning socialisation and environmental enrichment in crated farrowing and nursing pens has been shown to reduce stress relating to weaning and post-weaning aggression in pigs intended for slaughter (Ko et al., 2020). However, the majority of the studies reported on mixing and co-mingling of piglets during the nursing period have investigated systems where several sows and their piglets are housed together in groups or systems with individual sow housing where sows are crated. Reports on the effects of mixing and co-mingling of piglets in systems where sows are individually loose-housed during the nursing period are scarce (Van Kerschaver et al., 2023).

Genetic selection can influence behaviour, e.g. through breeding for less aggressive animals (Løvendahl et al., 2005; Turner et al., 2010; Peden et al., 2018; Rydhmer, 2020). Current breeding goals often focus on the same traits in most pig dam lines (i.e. improved litter size, piglet growth, piglet survival, sow and piglet health, etc.), but the production environment in which the animals are evaluated and selected may play an important role through indirect selection of traits not included in breeding goals, e.g. behaviours beneficial for coping in the specific production environment. Under the Swedish Animal Welfare Act 1988 (SFS 1988:534), individual stalls for sows during insemination and pregnancy and crated housing for sows during farrowing and nursing have long been banned in Sweden, unlike in many other countries (Einarsson et al., 2014). Therefore sows in Swedish pig production have been group-housed during insemination and pregnancy, and housed in individual loose-housing pens with their litters during farrowing and nursing, for several decades. Moreover, according to the Swedish Animal Welfare Act 1988 and the current version (SFS 2018:1192), all pigs must have access to straw at all times. Thus the Swedish Yorkshire genetic line selected for Sweden's rather unique production environment for sows (from an international point of view) may have been indirectly selected for behaviours beneficial for group housing of dry sows and loose-housed nursing. In parallel, sow lines such as Dutch Yorkshire (DY) may have been indirectly selected for behaviours beneficial in individual stalls (Horback & Parsons, 2016).

The objective of this study was to determine the effects of genetic line (breeding) and early-life social mixing (co-mingling) on female piglet activity, preferred pen location and social interactions pre- and post-weaning in a housing system with individually loose-housed sows. The hypotheses were that: (i) female piglets reared with access to unfamiliar piglets are more active and better prepared for the challenges related to weaning, as indicated by more initiation of social interactions and less time spent inactive in the piglet corner after weaning; and (ii) piglet activity, preferred pen location and social interactions differ between genetic lines evaluated and selected in different social environments.

Materials and methods

The experimental work was performed at the Swedish Livestock Research Centre, Lövsta, Uppsala, Sweden, during January 2018-January 2019. The experiment and all procedures involved were approved by the National Ethics Committee for Animal Experiments in Uppsala (Registration number: 5.8.18-16279/2017).

Animals, housing, and management

A total of 98 female piglets from two genetic dam lines, Dutch Yorkshire (DY; Topigs Norsvin distributed through Svenska Köttföretagen) and Swedish Yorkshire (SY; Nordic Genetics) (Lundeheim, 2017) were used. Only female piglets destined for gilt recruitment were included in the study, as the methods tested are intended to reduce damaging behaviours related to group housing in adult sows. The distribution of the 98 female piglets between genetic lines and early social mixing environments is shown in Table 1.

The female piglets were studied from birth until 10 weeks of age and originated from 26 litters divided over seven farrowing batches (A-G). In each farrowing batch, two pens were allocated to an access pen treatment (AP) and two pens to a control closed pen treatment (CP). The sow of each litter was moved into a loose-house farrowing and nursing pen approximately one week before expected farrowing. There were no gates for confining sows in the pen and thus all sows

Table 1. Number of female piglets (number of litters) of the genetic lines Dutch Yorkshire (DY) and Swedish Yorkshire (SY) allocated to two early social mixing environments, one where piglets had access to the sow and piglets in a neighbouring pen (AP) and one where piglets were confined to their own pen (CP) during the early socialisation phase (2–5 weeks of age).

	SY	DY	Total per treatment
Access pen (AP)	19 (5)	30 (7)	49 (12)
Closed pen (CP)	25 (8)	24 (6)	49 (14)
Total	44 (13)	54 (13)	98 (26)

were loose-housed at all times, including during and in the first days after farrowing. Multiparous sows of each genetic line were allocated randomly to either an AP or CP pen. The sow stayed in the pen until weaning of her piglets, at approximately five weeks (34.3 ± 1.86 days) after birth. The piglets stayed in the pen until approximately 10 weeks of age (69.2 ± 1.70 days).

Within 24 h after birth, four female piglets in each litter were selected for detailed observation. If there were more than four female piglets in the litter, four were randomly selected (but excluding the heaviest and/or the lightest). There were fewer than four female piglets in five of the 26 litters and in those cases only the female piglets available (2, 3, 3, 3, and 3 female piglets, respectively) were observed. For very large and very small litters, cross-fostering (within genetic line) was applied within two days after birth. However, none of the female piglets selected for the study was cross-fostered.

The pens measured 3.35 m × 2.00 m in total and were divided into three sections: a concrete-floored lying and feeding area (2.10 m × 2.00 m), a slatted dunging area (1.25 m × 2.00 m) and a piglet corner accessible only to the piglets with floor heating, a roof and a headlamp (Figure 1). The floor heating was turned on from before farrowing until one week after weaning. The heat lamp and the roof was always in place until week 3 after farrowing, and was taken away between weeks 3 and 5 after weaning depending primarily on season (i.e. climate differences between winter and summer) and piglet behaviour.

Each sow was provided with 15–20 kg chopped straw two days prior to the calculated date of farrowing. This straw was gradually lost through the slatted floor and an additional 0.5–1 kg straw was then provided, in accordance with common Swedish management routines to ensure that straw was always available for the sows. The pens were cleaned manually every morning. The sows were initially fed a standard commercial dry feed for lactating sows two times per day, via an automatic feeding system. When the piglets reached approximately 10 days of age, the feeding regime was extended to include one extra feed, i.e. the sows were then fed three times a day until the piglets were weaned. Dry feed adapted for piglets was provided on the floor, at a rate of 200 g per day, from when the piglets were approximately two weeks old, and an *ad libitum* feed dispenser was added in the piglet corner when the piglets reached approximately three weeks of age. Water was available *ad libitum* from two drinking nipples, placed one over the other, at 100 and 150 mm above the slatted floor (Figure 1).

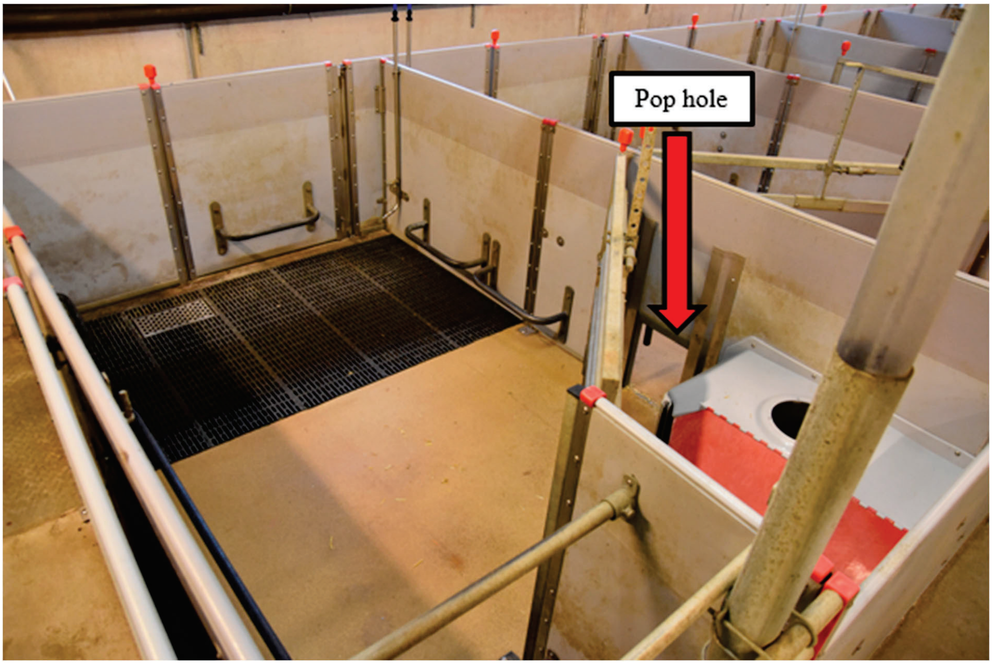


Figure 1. Pop-hole between two empty and cleaned access pens (AP).

All piglets received a 1 mL intramuscular injection of iron supplement (Uniferon, 200 mg/mL) and were ear-tagged at approximately four days of age (3.8 ± 0.78 days). The female piglets selected for observation were marked with ear-tags of individual colours other than yellow (all other piglets in the litter had yellow ear-tags) in preparation for behaviour observations. A second injection with the same amount of iron was administered at approximately two weeks of age (13.1 ± 1.79 days).

The health of the pigs was monitored continuously by farm staff and any issues arising were treated and documented. Piglets were weighed at birth and five weeks of age.

Early social mixing

The selected female piglets and their siblings were allocated to one of two different social housing environments. In two of the four pens in each farrowing unit, a pop-hole was made in the piglet corner connected to the neighbouring pen (Figure 1). This allowed piglets, but not sows, to move between the two pens, thus creating an extended social environment for the piglets in the AP treatment. The other two pens in each farrowing unit were conventional loose-house closed farrowing pens (CP), used as a control. Apart from the pop-hole, there were no differences between AP and CP housing. The early social mixing environment examined (between weeks 2 and 5) was chosen because it corresponds to the time when piglets in the wild meet new piglets (Jensen, 1986).

When the piglets reached approximately two weeks of age (13.1 ± 1.79 days; DY: 13.2 ± 1.65 days, SY: 13.0 ± 1.96 days), the pop-hole in the AP pens was opened. In the experimental design, balancing genetic line and early social mixing environment, four sows and their litters were included in each farrowing batch, two sows from each genetic line. One sow and her litter from each genetic line were then randomly allocated to each of the early social environment treatments. The intention was to have one CP per genetic line and one AP per genetic line for each batch in neighbouring pens, meaning that litters mixing in the AP treatment would be of different genetic lines. This was the case for 11 of the 13 litters (84.6%) in the AP treatment. The two AP treatment litters that did not meet the opposite genetic line met other litters not included in the study (one DY litter met crossbred SY*DY piglets in the neighbouring pen, while the other DY litter met another DY litter). The pop-hole was left open until weaning at five weeks of age (34.3 ± 1.86 days), after which the piglets were kept in their original pens and could not access the neighbouring pen again.

Behaviour and pen location observations

Each individual female piglet was treated as an observation unit and was observed on eight occasions during the study period (Figure 2).

Protocols for observation of body posture, preferred location in pen and social behaviour (Table 2) were developed in a pilot study (Vahlberg, 2019). For AP piglets, a distinction was made during the observations in weeks 3 and 4 on whether the piglet was in its home pen or the neighbouring pen when observations were made on body posture and location in pen. A similar distinction was not made for the AP piglets in weeks 2 and 5, as observations in week 2 were made on the day before opening the pop-hole and those in week 5 were made on the day after the pop-hole was closed and after the sow had been moved from the pen (Figure 2).

Social interactions were recorded in continuous observations, while body position and position in the pen were recorded with scan sampling. All behaviour observations were performed directly from outside the pen between 08:00 and 16:00 h, after the piglets were habituated to the observer (8 min). The observations started with scan sampling of all female piglets from each farrowing batch in each of the four pens, followed by continuous one-minute observations of two female piglets from each home pen. This routine was repeated until all female piglets had been scanned 17 times and

Event	**Birth**					**Weaning**					
Week of age	0	1	2	3	4	5	6	7	8	9	10
Early social mixing	Sow and litter mates only		**AP/CP**			With litter mates only					
Behaviour observations		**1**	**2***	**3**	**4**	**5***	**6**			**7**	**8**

Figure 2. Timing of behaviour observations and early social mixings (access to neighbouring pen (AP) or closed pen (CP)). *The observation in week 2 was made on the day before opening the pop-hole, while the observation in week 5 was made on the day after the pop-hole was closed and the sow was moved from the pen (at weaning).

Table 2. Ethogram of behaviours recorded with scan and continuous sampling.

Category	Variable	Definition	Analysis variable
Scan sampling			
Body posture	Lying on the side	Lying on the side, head/legs to the side	Lying
	Lying on the belly	Lying on the belly, with head nearly vertical, front legs not outspread to the side	Lying
	Sitting	Front feet on the ground, back legs in lying position	Not analysed – activity (sitting and standing/walking together) indirectly analysed through mirroring in the inactivity variable 'Lying'
	Standing/walking	Standing or walking on all four feet	Not analysed – activity (sitting and standing/walking together) indirectly analysed through mirroring in the inactivity variable 'Lying'
Location in pen	Lying area	Pig in the lying and feeding area	Not analysed – indirectly analysed through mirroring (lying and slatted area together) in the location variable 'Piglet corner'
	Slatted area	Pig in the slatted dunging area	Not analysed – indirectly analysed through mirroring (lying and slatted area together) in the location variable 'Piglet corner'
	Piglets corner	Pig in the heated piglet area	Piglets corner
Continuous sampling			
Social interactions, performing pig	Nosing	Snout touching other pig	Nosing
	Belly nosing	Pig nosing, sucking and/or massaging another pig's belly or throat with snout (not piglets on sow's teat)	Belly nosing
	Lifting	Snout on or under the body of another pig and lifting upwards. Including a range of lifting from gentle nudging to severe shovel.	Lifting
	Pushing	Pushing another pig with any part of the body in order to displace it, no biting	Pushing
	Climbing	At least one hoof/leg on the top of another pig	Climbing
	Mounting	Pig mounting another pig	Mounting
	Biting on body	Pig nibbling or biting another pig on body, excluding tail, vulva and ears.	Biting on body
	Tail biting	Pig with another pig's tail in its mouth	Tail biting
	Vulva biting	Snout touching/biting other pig's vulva	Vulva biting
	Ear biting	Pig with another pig's ear in its mouth	Ear biting
	Head knock	Approaching other pig with rapid head movement and open mouth	Head knock
	Performed bites total	Sum of 'Biting on body', 'Tail biting', 'Vulva biting and 'Ear biting'.	Biting total
	Performed social interactions – total	Sum of the above performed social interactions	Performed social interactions – total
Social interactions, receiving pig	Return approach	Receiving pig approaching the performing pig actively with head and/or snout.	Return approach
	Avoiding	Pig's head turning away or pig moving away from the performing pig	Avoiding
	No reaction	No change in body position or activity of the receiving pig. Only recorded if the receiving pig was awake or woke up by performing pigs initiation.	No reaction

Notes: For piglets in AP pens, which had access to the sow and piglets in the neighbouring pen, body posture and location in pen were recorded in both the home pen and the neighbouring pen on the observation occasions in weeks 3 and 4.

continuously observed twice (i.e. two minutes of continuous observation per occasion), giving a total of 136 scan samples and 16 min of continuous observation per female piglet for the eight observation occasions. If female piglets in AP pens were in the neighbouring pen during the observation, both pens were observed simultaneously. The nature of a social interaction is not defined solely by the behaviour of the performing pig, and must also consider the reaction of the receiving pig (McGlone, 1985; Newberry et al., 1988). Thus in addition to analyses of social behaviours, the reaction/behaviour of the receiving piglet was also recorded (as return approach, avoiding or no reaction) (Table 2).

The observations were made by two observers, with one main observer making 72.8% of the observations. To determine inter-observer reliability, both observers made simultaneous observations on six different occasions (112 direct observation minutes and 432 scans) and the degree of agreement was assessed using the kappa method in procedure FREQ in SAS. The agreement between the two observers was strong, with kappa values >0.95.

Statistical analyses

Statistical analyses were performed using SAS software (version 9.4 of the SAS system for Windows© 2016, SAS Institute Inc., Cary, NC, USA). The statistical unit assessed was animal (taking the litter into account) per observation occasion (week). Scan-recorded piglet activity and pen location were converted to percentage of scans per animal and observation occasion. Before the statistical analyses, continuously observed social behaviour variables, i.e. performing and receiving social behaviour, were transformed into binomial variables (female piglets performing each initiating social behaviour (or not) (Table 2), and female piglets responding to a social interaction with return approach (or not), avoiding (or not), or no reaction (or not) in each observation week).

Residuals of the continuous (not binomially distributed) dependent variables were examined for normal distribution using PROC UNIVARIATE considering Shapiro-Wilk's test and normal probability plots. All residual variables tested were found to be normally or approximately normally distributed. Results are presented as least squares means (LSM) with standard error (±SE), unless otherwise stated.

Statistical models were developed using step-backward selection of predictor effects where non-significant interactions and effects were deleted from the model. Statistical models were developed separately for general linear mixed models (normally distributed variables) and generalised mixed linear models (binomially distributed variables). Differences between genetic lines (DY and SY), early social mixing (AP and CP), and over time (1, 2, 3, 4, 5, 6, 9, 10 weeks of age) were analysed with PROC MIXED for continuous variables recorded with scan sampling (percentage of time lying and percentage of time in the piglet corner). Binomial variables recorded with continuous sampling (observations where female piglets initiated social interactions with lifting, pushing, climbing, mounting, biting on body, tail biting, vulva biting, ear biting, head knock and two additional variables, one merging all types of biting behaviour (Biting total) and one merging initiating any type of social behaviours (Performing Social interaction total), and observations where female piglets responded to a social interaction with return approach, avoiding, or no reaction) were analysed by PROC GLIMMIX, using binomial distribution and a logit link function. The following model was used for both continuous and binomial variables:

$$\begin{aligned} y = {} & \text{Genetic line} + \text{Early social mixing} + \text{Batch} \\ & + \text{Observation week} + \text{Genetic line} \\ & {}^{*}\text{Observation week} \\ & + \text{Early social mixing}\,{}^{*}\text{Observation week} \\ & + \text{PigID (genetic line/early social mixing/batch)} + e \end{aligned}$$

where y is the analysed variable, with genetic line (DY or SY), early social mixing (AP or CP), batch (A, B, C, D, E, F, G), observation week (1, 2, 3, 4, 5, 6, 9, 10), the interaction between genetic line and observation week, and the interaction between early social mixing and observation week included as fixed effects, and animal ($N = 98$ nested within genetic line, early social mixing, and batch) included as a repeated random effect; and e is random error effect. Due to the design of the study, the effect of animal nested within genetic line, early social mixing, and batch included the effect of birth litter.

The interaction between genetic line and early social mixing was tested during development of the statistical model but was found not to be significant ($p > 0.05$), so it was not included in the final model.

Differences between the genetic lines and between early social mixing treatments in piglet weight at birth, weaning (5 weeks) and 10 weeks of age were analysed with piglet as the statistical unit and with general linear mixed models using PROC MIXED with the following model:

$$\begin{aligned} y = {} & \text{Genetic line} + \text{Early social mixing} + \text{Batch} \\ & + \text{Litter (genetic line/early social mixing/batch)} + e \end{aligned}$$

where y is the analysed variable, with genetic line (DY or SY), early social mixing (AP or CP), batch (A, B, C, D, E, F, G) included as fixed effects, and litter ($N = 26$ nested within genetic line, early social mixing, and batch) included as a random effect; and e is random error effect.

Differences in litter size and piglet mortality between genetic lines and between early social mixing treatments were analysed with litter as the statistical unit. As no significant interactions between genetic line and early social mixing were found, pairwise analyses of genetic lines and of early social mixing environments were performed with general linear models using PROC GLM with the following model:

$$y = \text{Genetic line} + \text{Early social mixing} + \text{Batch} + e$$

where y is the analysed variable, with genetic line (DY or SY), early social mixing (AP or CP), batch (A, B, C, D, E F and G) and e as random error effect.

Differences in disease prevalence between genetic lines and between early social mixing treatments, differences between observation weeks and genetic lines in percentage of female piglets in neighbouring pens in the AP pens, and differences in percentage of observations in different pen locations in the neighbouring pen and body positions between genetic lines in the AP pens in weeks 3 and 4 were analysed with Chi square tests using PROC FREQ.

Table 3. Litter size, piglet mortality and mean piglet weight for Dutch Yorkshire (DY) and Swedish Yorkshire (SY) litters, and for litters in access pens (AP) and closed pens (CP) (LSM ± SE).

	AP LSM ± SE	CP LSM ± SE	*p*-value	SY LSM ± SE	DY LSM ± SE	*p*-value
No. of litters	13	13		12	14	
Litter size (no. of piglets)						
Birth (live-born)	15.6 ± 1.03	13.7 ± 1.02	0.220	11.5 ± 1.10	17.8 ± 0.99	0.001
5 weeks (weaning)	12.7 ± 0.71	10.4 ± 0.70	0.034	9.9 ± 0.75	13.3 ± 0.68	0.005
10 weeks	12.6 ± 0.70	10.3 ± 0.69	0.032	9.8 ± 0.75	13.1 ± 0.68	0.005
Piglet mortality (% dead of live-born until weaning)						
Piglet mortality (death of live-born until weaning, %)	16.4 ± 4.41	21.2 ± 4.33	0.459	13.1 ± 4.68	24.5 ± 4.23	0.098
Piglet weight (kg), no. of piglets given within brackets						
Birth (live-born)	1.5 ± 0.08 (209)	1.5 ± 0.08 (173)	0.837	1.6 ± 0.08 (132)	1.4 ± 0.07 (250)	0.078
5 weeks (weaning)	11.4 ± 0.26 (167)	11.5 ± 0.27 (132)	0.684	11.5 ± 0.29 (109)	11.3 ± 0.25 (190)	0.621
10 weeks	28.1 ± 0.74 (166)	27.3 ± 0.64 (130)	0.890	28.7 ± 0.74 (108)	27.3 ± 0.64 (188)	0.189

Notes: Litter size at 5 and 10 weeks includes piglets from the original birth litter even though some siblings of the female piglets studied were cross-fostered to other litters (not included in the study) in the same farrowing batch (6 SY, 29 ZY, 29 AP,6 CP, in total 35 cross-fostered piglets). Differences between genetic lines and social mixing treatments are indicated by the *p*-value.

Results

There was no difference in litter size at birth between litters born in AP and CP, but by 5 and 10 weeks of age litter size was significantly larger in AP, due to numerically higher piglet mortality in CP litters (although the difference was not significant due to large variation between litters). Average litter size was greater for DY sows compared with SY sows (Table 3).

The primary reason for medical treatment among the female piglets was leg problems, including joint inflammation, leg injuries and hoof damage. Of the DY piglets, 14.8% were treated for leg problems, compared with 4.6% of the SY piglets ($p = 0.095$). For female piglets housed in AP and CP, the percentage treated for leg problems was 10.2% in both treatments. Of the DY piglets, 13.5% were treated for illnesses other than leg problems, such as wounds or infections, compared with 2.4% of the SY piglets ($p = 0.056$). The corresponding value for AP piglets was 4.1%, compared with 12.2% for CP piglets CP ($p = 0.140$).

Location

Female piglets in AP pens were observed in the neighbouring pen for 24.1% of the time during week 3 observations, compared with 20.0% of the time in week 4 ($p = 0.045$). Of the female piglets in AP, SY piglets were located in the neighbouring pen for a smaller proportion of time (scans) than DY piglets (19.0% and 24.0%, respectively; $p = 0.017$). All female piglets in the AP pens were observed in the neighbouring pen at least once. In observation scans in weeks 3 and 4, AP piglets observed in the neighbouring pen spent 55.4% of the time lying, with no significant differences between the genetic lines. However, presence in the piglet corner of the neighbouring pen differed between genetic lines, in that DY female piglets spent 58.0% of the observed scans in the neighbouring pen located in the piglet corner, compared with 72.4% for SY female piglets ($p = 0.007$).

The female piglets observed in the present study spent the majority of their time located either in the lying area with the sow or in the piglet corner (Table 4). For time spent in the piglet corner, there were significant interactions between early social mixing and observation week ($p = 0.001$) (Figure 3), and between genetic line and observation week ($p = 0.005$) (Figure 4). There was no clear pattern in the differences between early social mixing or between genetic lines, but there were differences between weeks in how much time the female piglets spent in

Table 4. Descriptive statistics on percentage of scans (time) (in total 17 scans per female piglet and observation week, mean % ± standard deviation) spent by Dutch Yorkshire (DY) and Swedish Yorkshire (SY) female piglets, and by female piglets in access pens (AP) and control pens (CP), in different locations in the pen and in different body positions.

Variable	SY	DY	AP	CP	All
No. of female piglets	44	54	49	49	98
Location in pen					
Lying area	40.1 ± 23.41	45.4 ± 23.92	42.2 ± 22.87	43.8 ± 24.75	43.0 ± 23.83
Slatted area	17.6 ± 19.46	15.8 ± 18.35	17.3 ± 19.16	15.9 ± 18.57	16.6 ± 18.87
Piglet corner	42.3 ± 27.48	38.8 ± 27.07	40.4 ± 26.20	40.3 ± 28.38	40.3 ± 27.29
Body position					
Lying	62.1 ± 21.95	66.5 ± 18.65	63.6 ± 20.40	65.4 ± 20.19	64.5 ± 20.30
Sitting	2.3 ± 4.08	3.8 ± 6.13	2.9 ± 4.75	3.3 ± 5.91	3.1 ± 5.36
Standing/walking	35.6 ± 21.84	29.7 ± 17.45	33.5 ± 19.82	31.2 ± 19.65	32.3 ± 19.75

Note: For observations in week 3 and 4 after birth in AP pens, location in pen and body position were observed in both the home pen and the neighbouring pen.

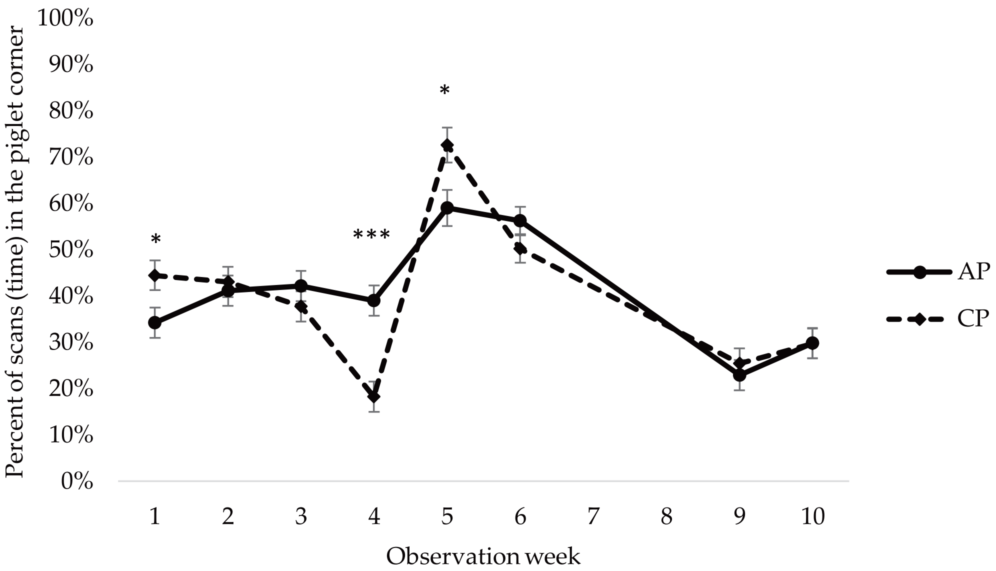


Figure 3. Percentage of scans (time) spent in the piglet corner by female piglets housed in access pens (AP) and closed pens (CP) in observation weeks 1–10. LSM ± SE. In total 17 scans per female piglet and observation week. For observations in weeks 3 and 4 in AP pens, when the piglets had access to both the home and neighbouring pen, observations in the piglet corner in both pens are included. Weaning occurred at week 5. $N = 784$ scans. Significance levels for pairwise differences within observation week are indicated: ***$p < 0.001$, *$0.01 < p < 0.05$.

the piglet corner. For example, there was a large increase in time spent in the piglet corner directly after weaning, especially for female piglets housed in CP (Figures 3 and 4). Prior to weaning, female piglets in the CP pens had been decreasing their time in the piglet corner. There was a corresponding increase in time spent in other areas of the pen, i.e. if the piglets were not in the piglet corner they were in the lying or slatted area.

Body position

All female piglets spent the majority of their time lying down (Table 4). For percentage of time lying, there was a significant interaction between early social mixing and observation week ($p = 0.001$). Pairwise comparisons within observation week indicated that female piglets housed in CP spent a larger percentage of their time lying in the last few weeks before weaning (which occurred at five weeks of age) and then showed a large decrease in time spent lying after weaning, whereas female piglets in AP did not alter their lying behaviour after weaning (Figure 5). There was also a significant interaction between observation week and genetic line ($p = 0.001$). Pairwise comarisons within observation week showed that DY female piglets spent a larger percentage of their time lying down from week 3 to week 6 after birth (Figure 6).

Social interactions

The most frequent social interaction initiated was nosing another pig, followed by interactions where the performing pig pushed or climbing on the receiving pig (Figure 7). The proportion of social interactions per initiating behaviour that were met with the response ‘no reaction’, ‘avoiding or ‘return approach’ is presented in Figure 8. SY female piglets showed ‘no reaction’ in response to a social interaction in a larger percentage of observations (88.2 ± 2.00%) than DY female piglets (78.9 ± 2.41%) ($p = 0.005$). There were no other significant effects of genetic line or early social mixing for any of the other performed or received social interactions analysed. There were no differences in the percentage of female piglets performing some kind of social interaction (‘performed social interactions total’) between the observation weeks, but the percentage of female piglets performing nosing at least once during the weekly observations increased gradually over time, from 31% in week 1 to 87% in week 10, for both DY and SY piglets and in both the AP and CP treatments ($p = 0.001$). Moreover, the

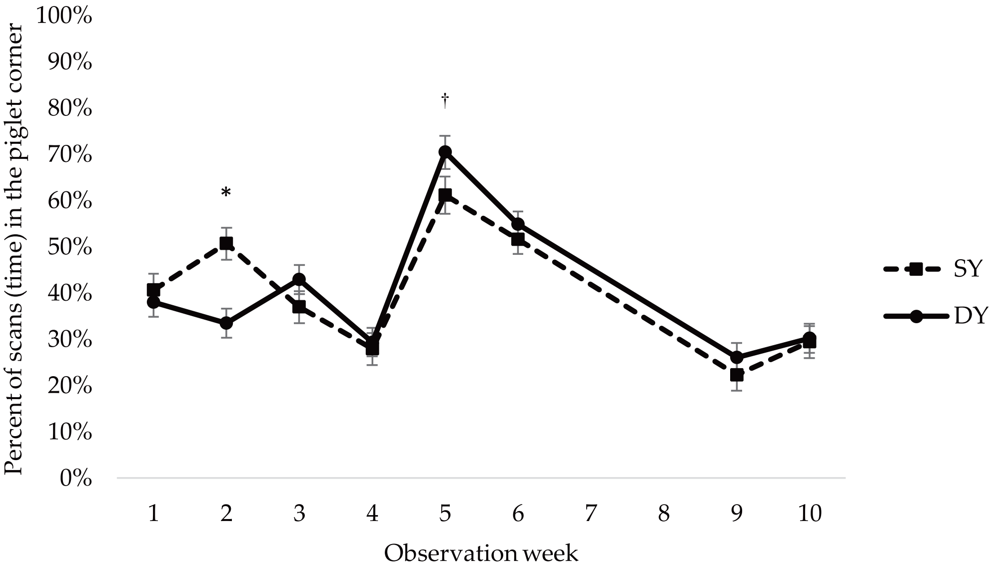


Figure 4. Percentage of scans (time) spent in the piglet corner by Swedish Yorkshire (SY) and Dutch Yorkshire (DY) female piglets in observation weeks 1–10. In total 17 scans per female piglet and observation week. LSM ± SE. For observations in weeks 3 and 4 in AP pens, when the piglets had access to both the home and neighbouring pen, observations in the piglet corner in both pens are included. Weaning occurred at week 5. $N = 784$ scans. Significance levels for pairwise differences within observation week are indicated: *$0.01 < p < 0.05$, †$0.05 < p < 0.1$.

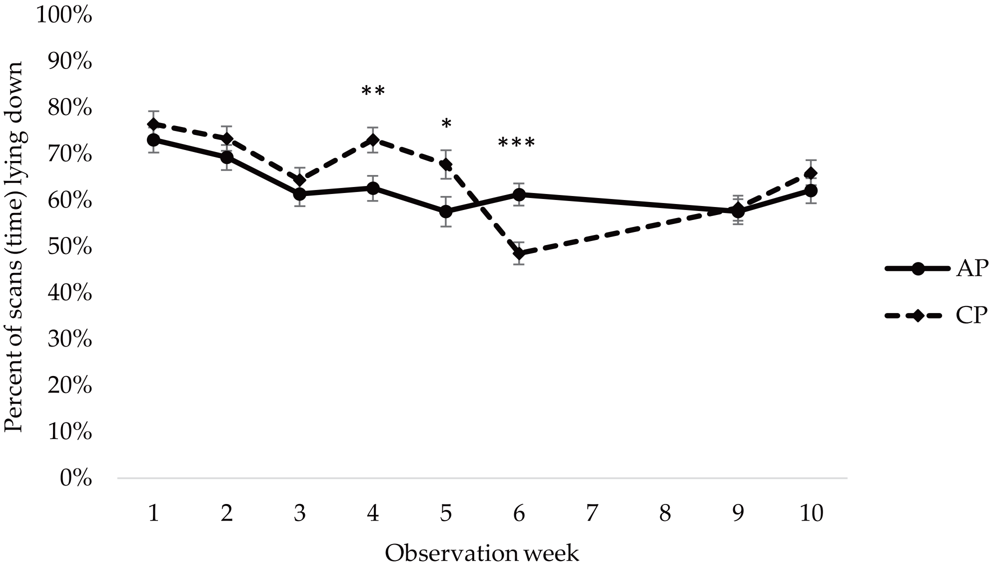


Figure 5. Percentage of scans (time) spent lying by female piglets housed in access pens (AP) and closed pens (CP) in observation weeks 1–10. In total 17 scans per female piglet and observation week. LSM ± SE. For observations in weeks 3 and 4 in AP pens, when the piglets had access to both the home and neighbouring pen, observations in both pens are included. Weaning occurred at week 5. $N = 784$ pig observation scans. Significance levels for pairwise differences within observation week are indicated: ***$p < 0.001$, **$0.001 < p < 0.01$, *$0.01 < p < 0.05$.

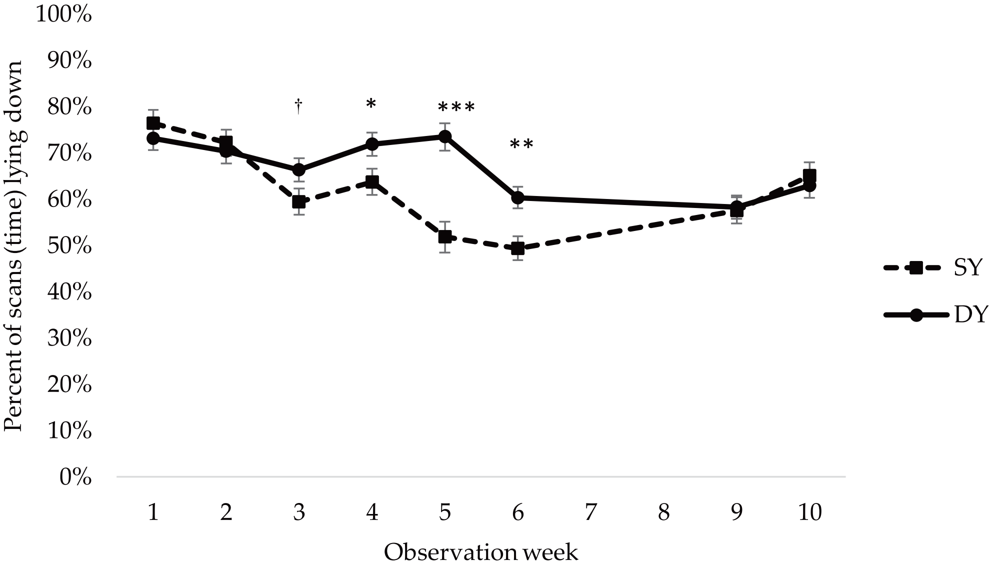


Figure 6. Percentage of scans (time) spent lying by Swedish Yorkshire (SY) and Dutch Yorkshire (DY) female piglets in observation weeks 1–10. In total 17 scans per female piglet and observation week. LSM ± SE. For observations in weeks 3 and 4 in AP pens, when the piglets had access to both the home and the neighbouring pen, observations in both pens are included. Weaning occurred at week 5. $N = 784$ scans. Significance levels for pairwise differences within observation week are indicated: $^{***}p < 0.001$, $^{**}0.001 < p < 0.01$, $^{*}0.01 < p < 0.05$, $^{\dagger}0.05 < p < 0.1$.

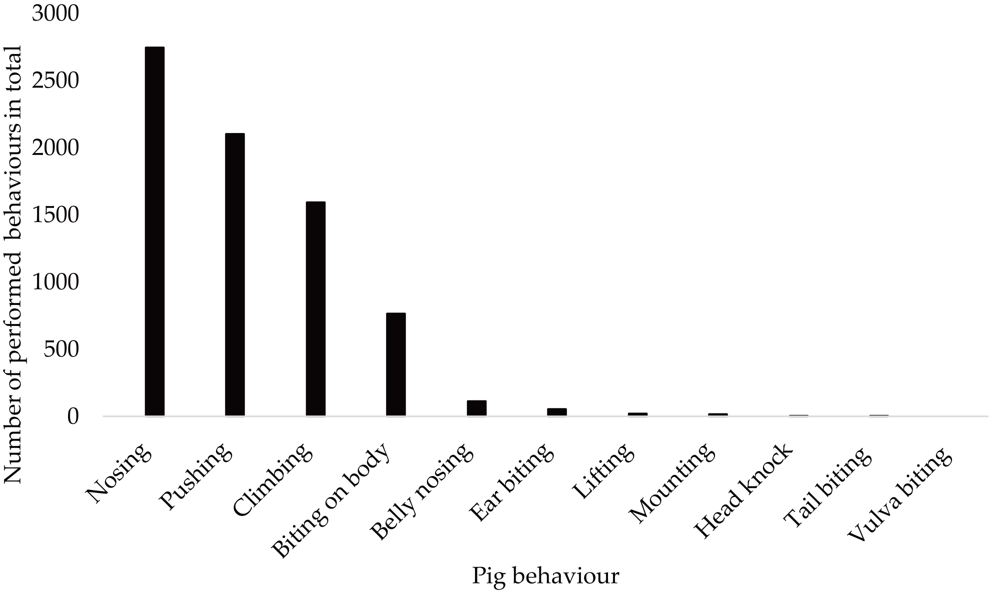


Figure 7. Descriptive statistics on total frequency of social interactions performed by the female piglets during the in total 1568 min (23.1 h) of continous observations of the female gilts in the study.

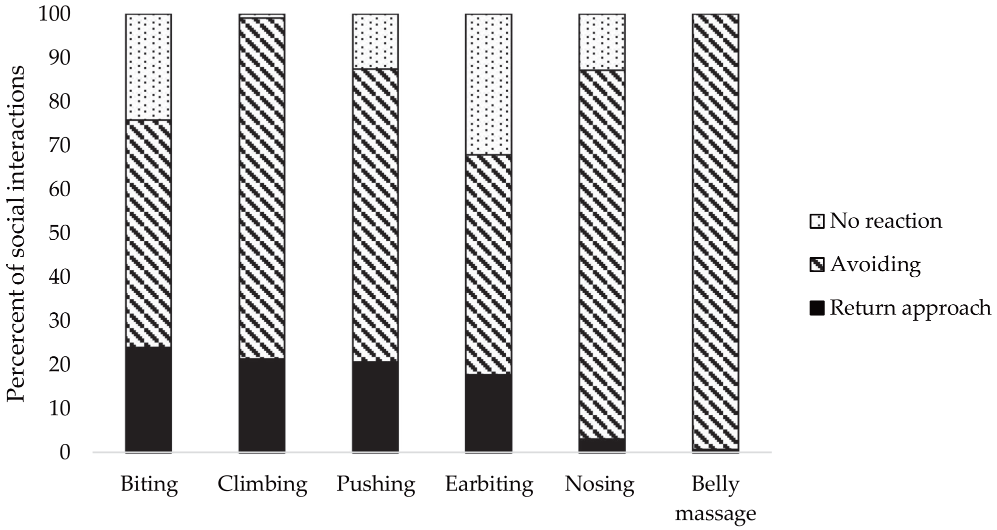


Figure 8. Percentage of the most frequent types of social interactions initiated (Figure 7) to which female piglets responded with a return approach, avoiding response, and no reaction.

percentage of female piglets performing biting (biting total) at least once during the weekly observations also increased gradually over time, from 8% in week 1 to 49% in week 10 ($p = 0.001$). In contrast, the percentage of female piglets initiating social interactions with climbing at least once during the weekly observations decreased gradually over time, from 61% in week 1 to 14% in week 10 ($p = 0.001$).

Discussion

The effects of early mixing and genetic line on female piglet activity, preferred pen location and social interactions pre- and post-weaning were compared under housing conditions feasible for implementing commercial pig production in Sweden. The key findings were effects of early mixing on changes in the behaviour of female piglets around weaning (greater behaviour change in CP piglets compared with AP piglets) and of genetic line on socialisation in the neighbouring pen (DY piglets spent a larger percentage of time in the neighbouring pen).

Weaning has frequently been reported to be challenging for piglets, causing e.g. deterioration in health and behaviour changes that have been linked to potential welfare problems and stress (Campbell et al., 2013; Matthews et al., 2016; Ko et al., 2020; Blavi et al., 2021; Van Kerschaver et al., 2023). In this study, female piglets housed in CP altered their time spent in the piglet corner and their lying behaviour after the sow had been moved from the pen to a larger extent than female piglets housed in AP. The increased time spent in the piglet corner after weaning seen in all piglets was probably caused by a combination of factors, such as seeking heat and social support from litter mates, but it was particularly noticeable in the CP treatment because the time in the piglet corner had been decreasing before weaning. Female piglets in the CP treatment decreased their time lying in the week after weaning, while the percentage of time lying remained stable around weaning for female piglets in the AP treatment. In combination, the altered lying behaviour observed for CP piglets and their greater use of the piglet corner may indicate that piglets in that treatment were more affected by weaning than piglets in AP. Potential reasons for this could be that AP pigs did not have the same attraction to the piglet corner in their home pen, as indicated by the finding that the AP piglets spent the majority of the weeks 3 and 4 scans in the piglet corner of the neighbouring pen, or that they were more accustomed to being away from their own mother and thus weaning was not as novel for them as for CP piglets. These results are in agreement with previous findings on differences in social behaviour and activity between socialised and unsocialised piglets (e.g. Kutzer et al., 2009; Salazar et al., 2018; Ko et al., 2020; Van Kerschaver et al., 2023). The findings of the present study support previous findings and shows that socialisation in piglets during nursing is beneficial for piglets handling challenges related to weaning also in commercial production environments with individually loose-housed sows and straw enrichment.

The female piglets in this study spent most of their time lying down, as also observed in several other studies (e.g. Hessel et al., 2006; Schrey et al., 2019). Regarding effects of early mixing on lying behaviour before weaning, the lower percentage of time lying among AP piglets in week 4 implied a higher level of activity that could have been due to the greater number of piglets available to play and be active with, and the larger space allowance created by the pophole (Chaloupková et al., 2007; Oostindjer et al., 2011; Singh et al., 2017; Salazar et al., 2018). This is partly supported by findings in previous studies where socialised piglets displayed a higher level of play behaviour from 14 days of age, hence displaying more active behaviour than non-socialised piglets (e.g. Salazar et al., 2018).

Regarding effects of genetic line on lying behaviour, DY female piglets spent more time lying down 3–6 weeks after birth than SY female piglets. A typical behaviour in ill pigs is reduced movement (Wilson et al., 2014). Thus one contributing explanation for the higher percentage of time spent lying by DY female piglets could be poorer health, as a higher percentage of those piglets were medically treated for leg problems or other illnesses than SY female piglets. There is no clear explanation for the poorer health in DY female piglets, but higher genetic potential for growth resulting in higher general sensitivity is probably part of the explanation.

An important element of the development of social behaviours in pigs is introduction of the piglet to unfamiliar sows and their piglets, corresponding to the reunion of sows and their piglets with the maternal social group that typically occurs at around 1–2 weeks after birth in wild and feral pigs (Jensen, 1986; Petersen et al., 1989; Wechsler, 1996). In the present study, female piglets in AP were frequently observed in the neighbouring pen, interacting with the piglets and sow in the other pen, as also seen in previous studies (Jensen & Redbo, 1987; Kutzer et al., 2009). Approximately 20% of AP female piglets were found in the neighbouring pen on the observation occasions when they had access to that pen. The percentage of time spent in the neighbouring pen differed between genetic lines, and was higher for DY compared with SY female piglets. This difference could be partly explained by the larger birth litters of DY compared with SY sows, since greater litter size increases piglet competition (Andersen et al., 2011; Kobek-Kjeldager et al., 2020). It is possible that DY female piglets took the opportunity to cross-suckle the sow in the neighbouring pen more often due to high competition at the udder of their own birth sow. This is supported by the high incidence and significantly higher proportion of cross-suckling in SY litters (i.e. DY piglets cross-suckled SY sows) found in a parallel pilot study assessing cross-suckling in the litters included in the present study (Lundahl, 2019). It is also supported by the finding in this study that during the observation scans where the AP female piglets were observed in the neighbouring pen in weeks 3 and 4, DY female piglets spent a lower percentage of scans in the piglet corner, and thus a higher percentage of the scan in pen locations where they could access the sow in the neighbouring pen.

In contrast to previous findings (e.g. Van Putten & Bure, 1997; Wattanakul et al., 1997; D'Eath, 2005) there were no differences in performance of social behaviours between genetic lines or social mixing environments investigated in this study. However, mapping of social behaviour over time indicated changes in social behaviour in the piglets with age. The percentage of female piglets performing nosing and biting increased over time, while the performance of climbing decreased, indicating gradual development of social behaviour during the five-week study period.

SY female piglets more often made no response to a social interaction than DY female piglets. Possible reasons are that SY female piglets were approached in social interactions to a lesser extent, that SY female piglets did not notice the social invitation, or that the threshold to respond to a social interaction was higher among SY than CP piglets. However, it is also likely that the smaller litter size in SY compared with DY litters contributed to the higher percentage of 'no response' reactions in SY piglets, as smaller litter size leads to less competition at the udder and fewer severe or agonistic social interactions between piglets. The difference could also be a result of the poorer health in DY compared with SY piglets, which may have caused more frequent agonistic social interactions among DY piglets due to e.g. pain and discomfort. However, since there were no other differences in social interactions performed or received between the genetic lines, the results imply that there are no major differences in social behaviour between female piglets of the two genetic lines.

Conclusions

This study revealed effects of early mixing on behaviour changes in female piglets around weaning and genetic line effects on socialisation with piglets in the neighbouring pen. Piglets housed in AP showed fewer signs of being affected by weaning than piglets housed in CP, as evidenced by smaller changes in behaviour from the week before, during and after weaning (weeks 2, 5 and 6, respectively) in AP piglets compared with CP piglets. Female piglets of the DY genetic line were more responsive to social interactions than female piglets of the SY line. The findings of this study support previous findings on favourable effects of early social mixing on piglets' behavioural response to weaning and confirm the findings for commercial production environments with individually loose-housed sows and straw enrichment. Moreover, this study indicates limited effects of genetic line on piglet response to weaning.

Acknowledgments

We would like to thank the farm staff at the Swedish Livestock Research Centre Lövsta (pig facility) for their support in conducting the experiment.

Author contributions

L.M. Backeman Hannius: Conceptualisation, Investigation, Data curation, Formal analysis, Methodology, Project administration, Visualisation, Writing – original draft, Writing – review & following. **L. Keeling:** Conceptualisation, Funding acquisition, Methodology, Supervision, Writing – review & following. **P. Ask-Gullstrand:** Investigation, Methodology, Project administration, Writing – review & following. **E. Verbeek:** Methodology, Formal analysis, Supervision, Writing – review & following. **A. Wallenbeck:** Conceptualisation, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualisation, Writing – review & following. All authors have read and agreed to the published version of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This research was funded by FORMAS, reference number: 2016-01787.

ORCID

Linda Marie Backeman Hannius http://orcid.org/0000-0003-1533-9966
Linda Keeling http://orcid.org/0000-0003-2629-0117
Patricia Ask-Gullstrand http://orcid.org/0000-0002-7450-8208
Else Verbeek http://orcid.org/0000-0002-1223-3480
Anna Wallenbeck http://orcid.org/0000-0001-8012-2849

References

Andersen, I. L., Nævdal, E. & Bøe, K. E. (2011). Maternal investment, sibling competition, and offspring survival with increasing litter size and parity in pigs (Sus scrofa). *Behavioral Ecology and Sociobiology*, 65, 1159–1167. doi:10.1007/s00265-010-1128-4.

Arey, D. S. & Edwards, S. A. (1998). Factors influencing aggression between sows after mixing and the consequences for welfare and production. *Livestock Production Science*, 56, 61–70.

Blavi, L., Solà-Oriol, D., Llonch, P., López-Vergé, S., Martín-Orúe, S. M. & Pérez, J. F. (2021). Management and feeding strategies in early life to increase piglet performance and welfare around weaning: a review. *Animals*, 11, 302. doi:10.3390/ani11020302.

Campbell, J. M., Crenshaw, J. D. & Polo, J. (2013). The biological stress of early weaned piglets. *Journal of Animal Science and Biotechnology*, 4, 1–4. doi:10.1186/2049-1891-4-19.

Chaloupková, H., Illmann, G., Bartoš, L. & Špinka, M. (2007). The effect of pre-weaning housing on the play and agonistic behaviour of domestic pigs. *Applied Animal Behaviour Science*, 103, 25–34. doi:10.1016/j.applanim.2006.04.020.

D'Eath, R. B. (2005). Socialising piglets before weaning improves social hierarchy formation when pigs are mixed post-weaning. *Applied Animal Behaviour Science*, 93, 199–211. doi:10.1016/j.applanim.2004.11.019.

Einarsson, S., Sjunnesson, Y., Hultén, F., Eliasson-Selling, L., Dalin, A. M., Lundeheim, N. & Magnusson, U. (2014). A 25 years experience of group-housed sows-reproduction in animal welfare-friendly systems. *Acta Veterinaria Scandinavica*, 56, 37–45. doi:10.1186/1751-0147-56-37.

Graves, H. B. (1984). Behavior and ecology of wild and feral swine (Sus scrofa). *Journal of Animal Science*, 58, 482–492. doi:10.2527/jas1984.582482x.

Greenwood, E. C., Plush, K. J., van Wettere, W. H. E. J. & Hughes, P. E. (2014). Hierarchy formation in newly mixed, group housed sows and management strategies aimed at reducing its impact. *Applied Animal Behaviour Science*, 160, 1–11. doi:10.1016/j.applanim.2014.09.011.

Hessel, E. F., Reiners, K. & Van Den Weghe, H. F. A. (2006). Socializing piglets before weaning: effects on behavior of lactating sows, pre- and postweaning behavior, and performance of piglets. *Journal of Animal Science*, 84, 2847–2855. doi:10.2527/jas.2005-606.

Horback, K. M. & Parsons, T. D. (2016). Temporal stability of personality traits in group-housed gestating sows. *Animal*, 10, 1351–1359. doi:10.1017/S1751731116000215.

Jensen, P. (1986). Observations on the maternal behaviour of free-ranging domestic pigs. *Applied Animal Behaviour Science*, 16, 131–142. doi:10.1016/0168-1591(86)90105-X.

Jensen, P. & Redbo, I. (1987). Behaviour during nest leaving in free-ranging domestic pigs. *Applied Animal Behaviour Science*, 18, 355–362. doi:10.1016/0168-1591(87)90229-2.

Ko, H. L., Chongb, Q., Escribanoa, D., Camerlink, I., Mantecaa, X. & Llonch, P. (2020). Pre-weaning socialization and environmental enrichment affect life-long response to regrouping in commercially-reared pigs. *Applied Animal Behaviour Science*, 229, 105044.

Kobek-Kjeldager, C., Moustsen, V. A., Theil, P. K. & Pedersen, L. J. (2020). Effect of litter size, milk replacer and housing on behaviour and welfare related to sibling competition in litters from hyper-prolific sows. *Applied Animal Behaviour Science*, 230, 105032. doi:10.1016/j.applanim.2020.105032.

Kutzer, T., Bünger, B., Kjaer, J. B. & Schrader, L. (2009). Effects of early contact between non-littermate piglets and of the complexity of farrowing conditions on social behaviour and weight gain. *Applied Animal Behaviour Science*, 121, 16–24. doi:10.1016/j.applanim.2009.08.004.

Løvendahl, P., Damgaard, L. H., Nielsen, B. L., Thodberg, K., Su, G. & Rydhmer, L. (2005). Aggressive behaviour of sows at mixing and maternal behaviour are heritable and genetically correlated traits. *Livestock Production Science*, (93), 73–85. doi:10.1016/j.livprodsci.2004.11.008.

Lundahl, I. (2019). *Differences in nursing behavior comparing Swedish and Dutch Yorkshire breeds – in nursing pens where the piglets have access to the sow and piglets in the neighbor nursing pen*. Bachelor thesis, Department of Animal Environment and Health, Swedish University of agricultural sciences. Available at: http://urn.kb.se/resolve?urn = urn:nbn:se:slu:epsilon-s-11024.

Lundeheim, N. (2017). *The rise and fall of Swedish pig breeding - pros and cons with genes from abroad*. XVIII Baltic Animal Breeding Conferene, May 30–31, Lithuania.

Matthews, S. G., Miller, A. L., Clapp, J., Plötz, T. & Kyriazakis, I. (2016). Early detection of health and welfare compromises through automated detection of behavioural changes in pigs. *The Veterinary Journal*, 217, 43–51. doi:10.1016/j.tvjl.2016.09.005.

McGlone, J. J. (1985). A quantitative ethogram of aggressive and submissive behaviors in recently regrouped pigs. *Journal of Animal Science*, 61, 559–565. doi:10.2527/jas1985.613556x.

Newberry, R. C., Wood-Gush, D. G. M. & Hall, J. W. (1988). Playful behaviour of piglets. *Behavioural Processes*, 17, 205–216. doi:10.1016/0376-6357(88)90004-6.

Oostindjer, M., van den Brand, H., Kemp, B. & Bolhuis, J. E. (2011). Effects of environmental enrichment and loose housing of lactating sows on piglet behaviour before and after weaning. *Applied Animal Behaviour Science*, 134, 31–41. doi:10.1016/j.applanim.2011.06.011.

Peden, R. S. E., Turner, S. P., Boyle, L. A. & Camerlink, I. (2018). The translation of animal welfare research into practice: the case of mixing aggression between pigs. *Applied Animal Behaviour Science*, 204, 1–9. doi:10.1016/j.applanim.2018.03.003.

Petersen, H. V., Vestergaard, K. & Jensen, P. (1989). Integration of piglets into social groups of free-ranging domestic pigs. *Applied Animal Behaviour Science*, 23, 223–236. doi:10.1016/0168-1591(89)90113-5.

Rydhmer, L. (2020). Advances in understanding the genetics of pig behaviour. In S. Edwards (Ed.), *Understanding the Behaviour and Improving the Welfare of Pigs* (1st ed.) (pp. 3–26). London: Burleigh Dodds Science Publishing). doi:10.1201/9781003048220.

Salazar, L. C., Ko, H. L., Yang, C. H., Llonch, L., Manteca, X., Camerlink, I. & Llonch, P. (2018). Early socialisation as strategy to increase piglets' social skills in intensive farming conditions. *Applied Animal Behaviour Science*, 206, 25–31. doi:10.1016/j.applanim.2018.05.033.

Schrey, L., Kemper, N. & Fels, M. (2019). Behaviour and skin injuries of piglets originating from a novel group farrowing system before and after weaning. *Agriculture*, 9, 93. doi:10.3390/agriculture9050093.

Singh, C., Verdon, M., Cronin, G. M. & Hemsworth, P. H. (2017). The behaviour and welfare of sows and piglets in farrowing crates or lactation pens. *Animal*, 11, 1210–1221. doi:10.1017/S1751731116002573.

Turner, S., D'Eath, R., Roehe, R. & Lawrence, A. (2010). Selection against aggressiveness in pigs at re-grouping: practical application and implications for long-term behavioural patterns. *Animal Welfare*, 19(S1), 123–132. doi:10.1017/S0962728600002323.

Vahlberg, J. (2019). *Difference in health and behaviour between two different pig line crosses*. Master of Science thesis, Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences. Available at: http://urn.kb.se/resolve?urn = urn:nbn:se:slu:epsilon-s-10300.

Van Kerschaver, C., Turpin, D., Michiels, J. & Pluske, J. (2023). Reducing weaning stress in piglets by pre-weaning socialization and gradual separation from the sow: a review. *Animals*, 13, 1644. doi:10.3390/ani13101644.

Van Putten, G. & Bure, R. G. (1997). Preparing gilts for group housing by increasing their social skills. *Applied Animal Behaviour Science*, 54, 173–183.

Wattanakul, W., Stewart, A. H., Edwards, S. A. & English, P. R. (1997). Effects of grouping piglets and changing sow location on suckling behaviour and performance. *Applied Animal Behaviour Science*, 55, 21–35. doi:10.1016/S0168-1591(97)00020-8.

Wechsler, B. (1996). Rearing pigs in species-specific family groups. *Animal Welfare*, 5, 25–35.

Wilson, R., Holyoake, P., Cronin, G. & Doyle, R. (2014). Managing animal wellbeing: a preliminary survey of pig farmers. *Australian Veterinary Journal*, 92, 206–212. doi:10.1111/avj.12169.

Animal 18 (2024) 101349

Contents lists available at ScienceDirect

Animal

The international journal of animal biosciences

Friend or foe: effects of social experience and genetic line on responses of young gilts in a social challenge paired interaction test

L.M. Backeman Hannius *, L. Keeling, D. de Oliveira, C. Anderson, A. Wallenbeck

Department of Applied Animal Science and Welfare, Swedish University of Agricultural Sciences, Box 7024, 750 07 Uppsala, Sweden

ARTICLE INFO

Article history:
Received 6 February 2024
Revised 22 September 2024
Accepted 27 September 2024
Available online 4 October 2024

Keywords:
Behaviour
Breed
Pig
Social mixing
Welfare

ABSTRACT

The increased focus on group housing of sows in commercial pig production emphasises the importance of saving appropriate gilts which later become sows that are well-adapted to group housing systems. This study aimed to assess the short-term effects of social mixing experience and genetic line on social and exploration responses of young gilts in standardised 3-min social challenge paired interaction tests. The study included 96 gilts, from 26 litters, of two different genetic lines (Swedish Yorkshire and Dutch Yorkshire). These lines were chosen because the dam lines have been selected in group-housed and individual stall systems, respectively, a background which was hypothesised to have modified their social behaviour over time. The gilts were subjected to different early (opportunity to co-mingle with piglets in the neighbouring farrowing pen vs. no opportunity to co-mingle) and late (mixed with unfamiliar piglets at weaning vs. kept with familiar littermates after weaning) social mixing treatments, to test whether the enhanced social experience was beneficial in a socially challenging situation. Paired interaction tests were conducted at 5 and 20 weeks of age, and social and exploration behaviour of the gilts was recorded and analysed. The results showed that Swedish Yorkshire gilts explored the pen fittings more than Dutch Yorkshire gilts during the 5-week test, whereas Dutch Yorkshire gilts explored the pen fittings more than Swedish Yorkshire gilts during the 20-week test. No differences in play behaviour were found during the 5-week test, but in the 20-week test, gilts with early social mixing experience in their farrowing pen showed more locomotor play behaviour than gilts without this experience. Overall, these results suggest that genetic line and early social mixing experience can influence the social and exploration behaviours of young gilts in paired interaction tests. There was no support for the hypothesis that genetic selection in different housing systems has altered social behaviour, but it may have affected the level of exploration behaviour. There was little support for our prediction that early social experience has beneficial effects in a socially challenging situation.

Implications

A future where sows are group housed requires pigs to be well-adapted to this system, ensuring their own health, sustainability and welfare, as well as resource efficiency and economic sustainability. This study showed that socialisation and genetic line can partly influence pig behaviour in a social challenge test situation. These findings improve understanding of how pigs' social abilities develop and should be taken into account when developing management strategies.

Introduction

Wild boars (*Sus scrofa*) are highly social and live together in maternal groups with related females and their offspring (Petersen et al., 1989; Kaminski et al., 2005; Poteaux et al., 2009). In this social environment, pigs have the opportunity to create relationships and practise social behaviours with individuals other than littermates and the mother sow from approximately 10 days of age, when the sow reunites with the group after farrowing (Petersen et al., 1989; Kanaan et al., 2012, Salazar et al., 2018). Young females can thus form individualised social relationships that continue to adult age (Podgórski et al., 2014; Peden et al., 2018; Bieber et al., 2019).

The behavioural repertoire of domesticated pigs (*Sus scrofa domesticus*) has been documented to be as diverse as that of the wild boar (Stolba and Wood-Gush, 1989; D'Eath and Turner,

---

* Corresponding author.
E-mail address: linda.marie.hannius@slu.se (L.M. Backeman Hannius).

https://doi.org/10.1016/j.animal.2024.101349
1751-7311/

2009) and their behavioural needs and capacity are adapted to different social contexts at different ages. Domesticated pigs have similar social needs to their wild counterparts (Goumon et al., 2020), but their social behaviour has to some extent been altered through domestication and modern breeding (Rydhmer, 2021). For example, some pig dam lines have been evaluated and selected based on performance in individual stalls and others on performance in group housing systems. Thus, even though social ability has not been included as a breeding trait, sows may have been indirectly selected for social behaviours favourable for these different systems. This is the case for Swedish and Dutch Yorkshire lines (**SY** and **DY** respectively), where SY has been evaluated and selected in group housing dry sow systems since the 1980 s and DY in stall systems.

In housing systems for intensive piglet production, piglets have few opportunities to socialise with pigs outside their own litters during the nursing period. This leads to stress and fights when they are mixed with unfamiliar pigs after weaning, which has become a welfare problem in pig production (Coutellier et al., 2007; Colson et al., 2012; Turner et al., 2017). In commercial housing systems, early socialisation, where piglets in adjacent pens are given access to each other by opening barriers between the pens, has been shown to alter social behaviour in piglets. Examples of this are that while piglets with extra social experience are quicker to initiate fighting when meeting unfamiliar pigs (Salazar et al., 2018), they show reduced fighting, both number and duration of the fights, and new hierarchies are established faster in new groups after weaning (e.g. D'Eath, 2005; Kanaan et al., 2012; Salazar et al., 2018; Camerlink et al., 2019; Weller et al., 2019; Oldham et al., 2020). Moreover, piglets that have been socialised with piglets in a neighbouring pen show more appropriate social behaviours than piglets without such social experience (Weller et al., 2019). This ability of animals to optimise their social behaviour to the demands of their social environment is known as social ability (Varela et al., 2020; Taborsky, 2021), and it is a multifactorial trait (Dingemanse and Wolf, 2013). Evaluating the social ability of pigs in their home pen environment and group is time-consuming and difficult to standardise; however, the social ability of individual pigs can be evaluated in standardised tests (e.g. D'Eath and Pickup, 2002; D'Eath, 2004; Koolhaas et al., 2013; Camerlink et al., 2015; Camerlink et al., 2019; Turner et al., 2020). In such tests, the immediate reaction and social response of the individual are evaluated within the specific social context of the test. The evaluation includes both the general activity of the individual, e.g. explorative and play behaviour, and behaviour during any social interactions. In animal welfare research, play has been identified as a potential indicator of positive animal welfare (Lawrence, 1987; Held and Špinka, 2011) and locomotor play, in particular, can be seen in response to access to larger and/or novel areas in pigs of different ages (Rauw, 2013, Horback, 2014).

In line with European Union (**EU**) regulations, group housing of dry sows has been mandatory since 2013, while there are ongoing discussions on the adoption of group housing for farrowing sows. Group housing systems, which allow for interactions between adult sows and piglets, have not been thoroughly examined in terms of their impact on the social learning abilities of piglets.

The aim of this study was to assess the short-term effects of social mixing and genetic line of gilts reared in loose housing pens on the social and exploration response in standardised social challenge paired interaction tests. The starting hypothesis was that gilts with extra social mixing experience and gilts of the Swedish Yorkshire line would explore their surroundings more, perform more locomotor play behaviour (associated with higher behavioural flexibility) and be more active and reactive in social interactions during paired interaction tests at both 5 and 20 weeks of age, compared with gilts of the Dutch Yorkshire line.

Material and methods

The study was performed at the Swedish Livestock Research Centre, Lövsta, Uppsala, Sweden, during February 2018–April 2019.

Animals, housing and management

This study included 96 gilts of two different genetic lines; 100% Swedish Yorkshire (SY) or at least 75% Dutch Yorkshire (DY). The gilts originated from 26 litters divided over seven batches (A-G) (i.e. 3 or 4 litters per batch) with the first batch born in January and the last in November 2018. These litters and their mother sows were housed in farrowing pens (total size: 3.35m × 2.0 m) including a concrete lying and feeding area (2.1 m × 2.0 m), a dunging area consisting of a slatted floor (1.25 m × 2.0 m) and a concrete-floored piglet corner with a heat lamp, a roof and floor heating, which only piglets could access. The average litter size at birth was 15 (15.0 ± 4.93 piglets, mean ± SE). At birth, the staff weighed (Table 1) and determined the sex of the piglets, and then four gilts from each litter were selected as focal animals for the study. All litters did not include four gilts; thus, the final number of gilts included in the study was 96. If there were more than four gilts in the litter, gilts with the best vitality, excluding the heaviest and the lightest gilts in the litter, were selected. For easier identification, the focal gilts of this study received ear tags of another colour (blue, red, white, green) than the colour (yellow) that the other piglets in the litter had. At the same time as the ear-tagging (3.9 ± 0.78 days), an iron supplement intramuscular injection of 1 mL (Uniferon, 200 mg/mL) was given. At approximately 2 weeks of age (13.1 ± 1.79 days), a second injection of the same amount of iron supplement was administrated.

The pens were manually cleaned every morning. Two days before the estimated date of farrowing, the sows were provided with straw (approximately 15–20 kg of chopped straw). Due to the slatted floor in the pen, the amount of straw gradually decreased and, as straw should always be available for sow and piglets in a farrowing pen (according to common Swedish management routines), additional straw was provided when needed. Sows were fed a standard commercial dry feed for lactating sows twice daily until the piglets were approximately 10 days old, and thereafter, sows were then fed three times a day until weaning. Dry creep feed (200 g per pig per day) for piglets was provided on the floor in the piglet corner, from when the piglets were about 2 weeks old. An *ad libitum* feeder was added in the piglet corner when the piglets reached approximately 3 weeks of age. The sow and the piglets had *ad libitum* water supply from two drinking nipples, placed at 0.1 m and 0.15 m above the slatted floor.

The sow stayed in the pen with the piglets until weaning, at approximately 5 weeks (34.3 ± 1.87 days) after the birth of the piglets. Piglets were individually weighed at weaning and at 9 weeks of age (Table 1). The piglets stayed in the pen until approximately 10 weeks of age (69.2 ± 1.72 days), when they were moved to a growing stable, focal gilts were separated out from the rest of the litter and housed in groups of four gilts per pen. The grower pens (3.96 m × 1.80 m) consisted of a concrete-floored lying and feeding area, and a slatted dunging area measuring 1.80 m × 1.00 m. The slatted dunging area was elevated 0.18 m from the concrete floor. The gilts were provided with dry feed three times per day, according to a standard feeding regime for breeding gilts, in the feeding trough (1.80 m × 0.23 × 0.15 m) placed along the short side and at the opposite end of the pen to the slatted floor. Water was available *ad libitum* from two drinking nipples, placed one over the other, at 0.43 m and 0.63 m above the slatted floor. Each pen was manually cleaned every morning and provided with approximately 350 g of straw each day. The health of the pigs was moni-

Table 1
Pig birth weights, weight at 5 weeks of age and weight at 9 weeks of age per genetic line (Swedish Yorkshire or Dutch Yorkshire), early social mixing (Access pen or Control pen) and late social mixing (Intact group or Mixed group).

	Weights of focal gilts						
	Total	Genetic line		Early social mixing		Late social mixing	
		SY	DY	AP	CP	IG	MG
N	96 gilts	42 gilts	54 gilts	49 gilts	47 gilts	50 gilts	46 gilts
(Mean ± SD)							
Birth weight	1.6 ± 0.26	1.7 ± 0.22	1.5 ± 0.28	1.6 ± 0.25	1.6 ± 0.28	1.5 ± 0.22	1.7 ± 0.26
Weight at 5 weeks of age	11.9 ± 2.11	12.2 ± 1.73	11.6 ± 2.35	11.8 ± 2.14	11.9 ± 2.10	11.6 ± 2.25	12.1 ± 1.95
Weight at 9 weeks of age	28.9 ± 4.26	29.3 ± 3.50	28.5 ± 4.78	29.3 ± 4.10	28.5 ± 4.43	28.2 ± 4.56	29.6 ± 3.82

Abbreviations: SY = Swedish Yorkshire; DY = Dutch Yorkshire; AP = Access pen; CP = Control pen; IG = Intact group; MG = Mixed group.

tored daily by farm staff, and any deviation from normal health was treated and documented.

Early social mixing treatments

In each farrowing batch, two litters were assigned to an early socialisation treatment, and two were assigned to a control treatment. A pop-hole (0.35 m × 0.30 m) was placed in the piglet corner between two pens (Fig. 1) making it possible for piglets, but not sows, to move between the two pens, thus creating an extended co-mingling social mixing environment) for the litters in the access pen (**AP** treatment). The pop-hole was opened when the litters reached 2 weeks of age (13.1 ± 1.79 days), which corresponds to the time when piglets would socialise with new piglets in a sow group in the wild (Jensen, 1986) and hence provided a relatively natural early social mixing environment in a conventional setting. The pop-hole was closed at weaning.

The other two pens in each farrowing batch did not have a pop hole and were used for the control treatment (**CP**). The design was balanced with two AP and two CP pens per batch, and two DY and two SY pens per batch, which meant that the piglets in the AP treatment met piglets of the other genetic line. However, due to the lack of available SY litters, two of the 13 litters of piglets in the AP treatment did not have the opportunity to co-mingle with a litter of the opposite breed. Instead, two DY litters met and co-mingled in the AP treatment in one batch, while in another batch, a DY litter met and co-mingled with a crossbreed litter (SY*DY piglets). The litter of SY*DY piglets was not included in the analysis.

Late social mixing treatments

At approximately 10 weeks of age (67.9 ± 7.66 days), focal gilts were moved to an experimental growing pig stable and allocated into groups of four in one of two late social mixing treatments. Selected gilts were either placed in an intact group (**IG**), where they were housed with gilts from their own farrowing litter, or allocated to groups of four with gilts from two birth litters so that each gilt was mixed with one familiar and two unfamiliar gilts in mixed groups (**MG**). The remaining piglets left the study.

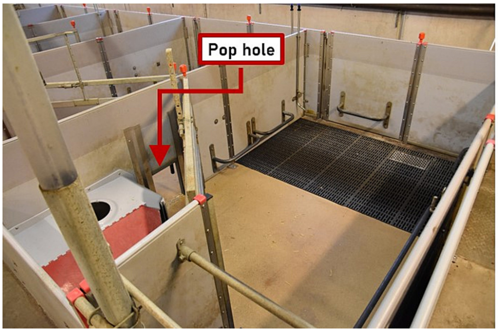


Fig. 1. Picture of empty and cleaned access pens (AP), created from conventional loose housing farrowing pens for pigs with a pop-hole located between the piglet corner in each pen.

This design resulted in four combinations of social experience balanced over genetic lines:

- Early social experience AP and late social experience MG (11 SY gilts and 15 DY gilts)
- Early social experience AP but no late social experience IG (8 SY gilts and 15 DY gilts)
- No early social experience CP, but late social experience MG (12 SY gilts and 8 DY gilts)
- No early social experience CP and no late social experience IG (11 SY gilts and 16 DY gilts)

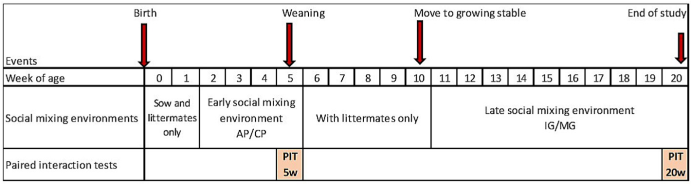
An overview of the experimental design is given in Fig. 2.

Paired interaction tests

Paired interaction test at 5 weeks of age

At weaning, when the gilts were approximately 5 weeks old, the first paired interaction test (designated PIT5w) took place. Each focal gilt was paired with an unfamiliar opponent gilt, reared in the same farrowing unit and farrowing batch, but from a regular conventional pen and from a litter without any of the focal gilts included in the study. Gilts were weighed the day before testing, and the opponent gilt had as similar weight as possible to the focal gilt (0.1 ± 1.78 kg weight difference). The paired interaction test (**PIT**) at 5 weeks was performed in the farrowing stable where the gilts were held, in a separate arena unfamiliar to all gilts (Fig. 3). The test arena (7.5 m × 1.5 m) had a concrete floor (5.0 m × 1.5 m) and a metal tread plate (covering the manure system) at each end of the area (1.25 m × 1.5 m each). They were not habituated to the test area.

The focal gilt and the opponent gilt were taken separately from their home pens and guided using a driving board to separate sides of the test arena. A technician thereafter started the PIT at 5 weeks by opening the gate separating the pigs so that they both had access to the whole test arena. The interaction test lasted 3 min, after which the focal gilt and the opponent gilt were guided back to their home pens. A camera (Garmin VIRB Ultra 30) located on the focal gilt side of the test pen was used to record the test. A technician stood outside the test arena to intervene if the social interactions became too aggressive or stressful and therefore overstepped the endpoints. The endpoint and termination of the ongoing PIT were reached if the pigs caused puncture wounds, injuries, or harmed themselves by slipping on the surface. Intervention was however never needed.



Week of age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Events	Birth					Weaning					Move to growing stable										End of study
Social mixing environments	Sow and littermates only		Early social mixing environment AP/CP				With littermates only					Late social mixing environment IG/MG									
Paired interaction tests						PIT 5w															PIT 20w

Fig. 2. Timing of early social mixing environment (Access Pen (AP) or Control pen (CP)), late social mixing environment (Mixed group (MG) or Intact group (IG) and paired interaction tests (PITs) in the gilt's life in relation to weeks of age.

Fig. 3. The test arena for pigs in the paired interaction test at 5 weeks of age (PIT5w).

Paired interaction test at 20 weeks of age

When the gilts were 20 weeks old, the second paired interaction test (PIT20w) took place in a new test arena, located in the corridor outside the stable. The area was enclosed by movable gates that were 0.91 m high (Fig. 4). The test arena measured 10.25 m × 3. 50 m and had a concrete floor, although about one-third of the floor consisted of metal tread plates. As previously, the gilts were not habituated to the test arena.

The two gilts participating in the test were taken from their pens and placed in starting pens on either side of the test arena. Two technicians then opened the gates to the test arena so that the gilts entered the arena at the same time. The gate to the test arena was closed when each gilt had entered the arena with all legs. In contrast to the PIT at 5 weeks of age, where the gilts met gilts from litters that were not included in the study, the gilts in the PIT at 20 weeks of age instead met another gilt from the study. The gilts were always matched with a gilt from the other early social environment, but limitations due to the number of gilts in each batch meant that genetic line and late social environment could not always be taken into consideration. The test lasted 3 min and was filmed using a camera (Garmin VIRB Ultra 30) placed approximately 1.5 m above the ground in a corner of the test pen. After the test, the gilts were separated using a driving board and led back to their home pens. Two technicians stood outside of the test arena ready to intervene if necessary, but intervention was never needed.

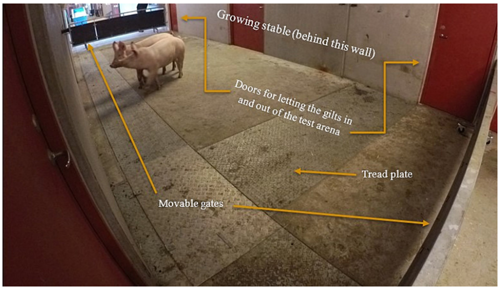


Fig. 4. The test arena for pigs in the paired interaction test at 20 weeks of age (PIT20w).

Behavioural observations

Behavioural observations were made from the videos recorded during both PIT occasions, and all observations were performed by the same trained observer. All focal gilts were continuously observed for 3 min. In the PIT at 5 weeks, the video analysis started when the door between the gilts was opened, while in the PIT at 20 weeks, the video analysis started when both gilts had all four legs within the test arena. As both gilts in the PIT at 20 weeks were focal animals, these films were analysed twice, once per focal gilt. All behaviours were observed continuously and recorded individually for each focal gilt and test (observation) minute. In the continuous recordings, a change in behaviour or a pause of a specific behaviour lasting at least 3 sec was set as a criterion for it to be recorded as a new behaviour. Social interactions were classified as an interaction between two pigs, and the gilt which was the performer (initiated the social behaviour) and the receiver (responded to the social behaviour) was noted. The event-logging software BORIS v. 7.9.8 – 2020-01-28 (Friard and Gamba, 2016) was used for all behavioural observations. Body posture and the distance between gilts, details of the first interaction, locomotor play behaviours, activity and social behaviours were recorded using an ethogram (Table 2), which was developed from ethograms used in previous studies (e.g. Xin et al., 1989; De Leeuw and Ekkel, 2004; Welfare Quality, 2009) and from pilot studies within the research project (Nihlstrand, 2016; Hannius, 2019; Vahlberg, 2019; Emriksson, 2021).

Statistical analyses

Data from BORIS were exported to and edited in Microsoft Excel 2016 for statistical analyses. The statistical analyses of the PIT at 5 weeks included 95 gilts, as data for one gilt of the genetic line SY in early social treatment CP were missing due to camera failure. In the PIT at 20 weeks analyses, 94 gilts were included, due to missing observations related to video quality for two gilts of the genetic line DY in the CP and MG treatment combinations. Statistical analyses were performed using the R software (R Core Team, 2021), implementing all models in the R package stats-package (R: The R Stats Package, 2021; R Core Team 2021). Level of significance was set at $P < 0.05$. The statistical models used were developed based on backward stepwise selection of effect, includ-

Table 2
Ethogram of behaviours recorded and variables analysed in the paired interaction test (PIT) carried out on gilts at 5 and 20 weeks of age.

Behaviour category	Variable name	Definition	Variable type in statistical analysis or reason for not analysed further
Body posture & distance – Scan sample every 15 s, statistical unit; observation minute per focal gilt			
	Lying on the belly	Lying on the belly, with head in a nearly vertical position, front legs not outspread to the side	Did not occur
	Lying on the side	Lying on the side, head/legs on the side	Did not occur
	Sitting	Front feet on the ground, back legs in lying position	Did not occur
	Standing	On all four feet, standing or walking	The focal gilts always stood up during recordings
	Distance	0 = The distance between the pigs is less than an equal size pig 1 = The distance between the pigs is greater than an equal size pig	Binary
First interaction – Recorded once per test, focal gilt statistical unit			
	Latency	Seconds from start of the test until first touch (snout touching the other pig)	Continuous (s)
	Meeting on focal gilt side	First touch appeared on the same side as the focal gilt started on	Binary
	Focal gilt approached first	The focal gilt was the first to approach (touch) the other pig	Binary
Locomotor play behaviour – continuous sampling, statistical unit; observation minute per focal gilt			
	Hop/spring	Jumping up and down in one spot while facing in one direction	Binary
	Scamper	A sudden forward movement of at least two hops in rapid succession	Binary (merged with "Sprint")
	Sprint	A sudden forward motion either towards or away from conspecific	Binary (merged with "Scamper")
	Pivot	Jumping or whirling around to face in a different direction	Binary
	Toss head	Exaggerated lateral displacement of the head and neck in the horizontal plane, involving at least one full movement to each side	Binary
	Play at all	Any of the play behaviours (hop/spring, scamper, pivot or toss head)	Binary
Activity – continuous sampling, statistical unit; observation minute per focal gilt			
	Explore pen fitting	Amount of times the snout touched the pen fittings	Continuous
	Explore pen floor	Amount of times the snout touched the pen floor	Continuous
Social interactions – statistical unit; observation minute per focal gilt			
Social interaction performing pig -continuous sampling			
	Nose to body	Snout touching the receiving pig's body	Binary
	Nibbling/biting	The pig nibbles or bites the receiving pig	Binary
	Climbing	Stepping and lying on top of the receiving pig	Binary
	Levering	The pig puts its snout under the body of the receiving pig and lifts the pig up in the air	Binary
	Pushing	Displacing the receiving pig by pushing any region of the body	Binary
	No sound	Either the pig is silent or it is not possible to identify where the sound is coming from	Binary
	Grunt	The pig is producing a low-frequency vocalisation	Binary
	Scream	The pig is screaming, barking or squealing	Binary
Social interaction receiving pig- continuous sampling			
	No reaction	No change in body position or activity	Binary
	Avoiding	Moving away from the performing pig	Binary
	Nose to body	Snout touching the receiving pig's body	Binary
	Pushing	Displacing the receiving pig by pushing any region of the body	Binary
	Nibbling/biting	The pig nibbles or bites the receiving pig	Binary
	No sound	Either the pig is silent or it is not possible to identify where the sound is coming from	Binary
	Grunt	The pig is producing a low-frequency vocalisation	Binary
	Scream	The pig is screaming, barking or squealing	Binary

ing all possible interactions between effects. The aim of model development was to create harmonised models for clusters of variables with the same characteristics, taking into account the statistical significance of the effects, best possible fit of the model (based on AIC and BIC) and biological relevance. PITs at 5 weeks and PITs at 20 weeks were analysed separately. Compared to the models for the PIT at 5-weeks, the models for the analyses of the PIT at 20 weeks also included effects of the late social mixing environment of the focal gilt, and the genetic line and late social environment of the opponent gilt. As the gilts in the PIT at 20 weeks always met a gilt with the opposite early social mixing treatment, this was not part of the model.

The response variables "Latency", "Meeting on focal gilt side" and "Focal gilt approached first" were analysed with focal gilt as the statistical unit. "Latency" was analysed with a Gaussian generalised linear model, while "Meeting on focal gilt side" (first touch on the same side as the focal gilt started: yes (1) or no (0)) and "Focal gilt approached first" (first touch by the focus gilt: yes (1) or no (0)) were analysed with binomial generalised linear models. For analyses of "Latency", "Meeting on focal gilt side" and "Focal gilt approached first" in the PIT at 5 weeks, genetic line and early social mixing environment were set as fixed effects, including interactions between the fixed effects. For the PIT at 20 weeks, genetic line, early social mixing environment, late social mixing environment, opponent's genetic line and opponent's late social mixing environment were set as fixed effects.

The response variables "Distance", "Play", "Performing social interactions", "Receiving social interactions", "Explore floor" and "Explore pen fitting" were analysed with observation minute per focal gilt as the statistical unit. "Distance" (percentage of 15-sec scans the gilts spent close to each other each minute) was analysed with a Gaussian generalised linear model. "Play" (performing during the observation minute: yes (1) or no (0)), "Performing social interactions" (performing during the observation minute: yes (1) or no (0)) and “Receiving social interactions” (receiving during the observation minute: yes (1) or no (0)) were analysed with binomial generalised linear models. “Explore floor” (counts per observation minute) and “Explore pen fitting” (counts per observation minute) were analysed with Poisson generalised linear models. For analyses of “Distance”, “Play”, “Performing social interactions”, “Receiving social interactions”, “Explore floor” and “Explore pen fitting” in the PIT at 5 weeks, genetic line, early social mixing environment and observation minute were set as fixed effects, including interactions between the fixed effects. For the PIT at 20 weeks, genetic line, early social mixing environment, late social mixing environment, observation minute, opponent’s genetic line and opponent’s late social mixing environment were set as fixed effects, including interactions between the fixed effects.

In order to compare classes of fixed effects and combinations of classes of interactions between fixed effects in all models, ANOVA tables were created using the function joint:tests from the R package emmeans (Lenth et al., 2022). *Posthoc* pairwise comparisons were carried out with the function emmeans from the emmeans package for the significant variables identified in the joint:test table. Resulting *P*-values were adjusted using the Bonferroni method.

Results

Descriptive statistics of gilt responses in the 5-week test are presented in Tables 3 and 4 and for the 20-week test in Tables 5 and 6.

Effects of genetic line and minute of interaction on gilt responses during the 5-week test

Treatment effects were observed for genetic line and minute of interaction, but not for early social mixing. The SY gilts explored the pen fittings more than the DY gilts (1.83 ± 0.11 and 1.30 ± 0.10 (LSMeans ± SE) times per observation minute, respectively (F = 12.70; df = 273; *P* < 0.001). Both SY and DY gilts explored the pen fittings more in the last observation minute of the test than in the first and second observation minute (1.3 ± 0.13, 1.4 ± 0.13, 1.9 ± 0.13 times per min (LSMeans ± SE) in observation minutes 1,2 and 3, respectively) (F = 6.26; df = 273; *P* = 0.002).

The gilts spent less time close together during the first observation minute of the test than during the second and third observation minutes (60.5 ± 2.16, 82.6 ± 2.16 and 79.1 ± 2.16% (LSMeans ± SE) in observation minutes 1,2 and 3, respectively) (F = 30.03; df = 273; *P* < 0.0001).

The response behaviour of receiving pigs to avoid a social interaction increased over the duration of the test (80.5 ± 2.93, 15.9 ± 3.97 and 25.3 ± 4.78% (LSMeans ± SE) in observation minutes 1, 2 and 3, respectively) (F = 4.29; df = 273; *P* = 0.014).

Effects of genetic line, minute of interaction and early and late social mixing on gilt responses during the 20-week test

Treatment effects were observed for genetic line, early social mixing and minute of interaction, but not for late social mixing. Gilts from the genetic line SY were closer to the opponent gilt than gilts from the DY line (73.8 ± 2.46 and 65.0 ± 2.30 (LSMeans ± SE) % of scans close the other pig per observation minute, respectively) (F = 6.89; df = 232; *P* = 0.009). Distance to the other pig varied between observation minutes of the test (69.3 ± 2.74, 79.1 ± 2.74 and 62.8 ± 2.74% (LSMeans ± SE) in observation minutes 1, 2 and 3, respectively) (F = 7.84; df = 232; *P* < 0.001), with gilts being close to each other most often during the second observation minute of the test.

Gilts with additional early social mixing experience were more likely to display locomotor play behaviours in the PIT at 20 weeks of age than gilts without (binary, i.e. percentage of gilts playing at least once during the observation period 59.2 ± 4.73 (AP) and 43.7 ± 5.78 (CP) % (LSMeans ± SE) (F = 4.12; df = 232; *P* = 0.042). The *P* of playing varied between the observation minutes (70.0 ± 5 .68, 42.1 ± 6.25 and 41.3 ± 6.32% (LSMeans ± SE) in observation minutes 1, 2 and 3, respectively) (F = 6.54; df = 232; *P* = 0.001), with gilts showing more locomotor play behaviour during the first observation minute.

The DY gilts explored the pen fittings more than the SY gilts (1.34 ± 0.11 and 0.93 ± 0.10 times per observation minute, respectively (LSMeans ± SE) (F = 7.75; df = 232; *P* = 0.005). Exploration of pen fittings increased over the duration of the test (0.8 ± 0.11, 1.0 ± 0.12 and 1.7 ± 0.15 times per minute (LSMeans ± SE) in observation minutes 1, 2 and 3, respectively) (F = 11.92; df = 232; *P* < 0.001), with more exploration in the last observation minute of the test compared with the 1first and second minutes.

Exploration of the floor also increased over time during the test (2.6 ± 0.19, 2.8 ± 0.20 and 3.9 ± 0.23 times per minute (LSMeans ± SE) in observation minutes 1, 2 and 3, respectively) (F = 13.23; df = 232; *P* < 0.001), and the gilts explored the pen floor more in the last observation minute of the test. Moreover, differences in exploration behaviour were observed in the interaction between genetic lines and late social mixing environments (F = 9.41; df = 232; *P* = 0.002) (Fig. 5).

Discussion

The initial hypothesis in this study was that gilts with extra social experience and gilts of the SY genetic line would exhibit greater exploration of their surroundings, engage in more locomo-

Table 3
Responses in the paired interaction test at 5 weeks of age for gilt of the genetic lines (Swedish Yorkshire or Dutch Yorkshire) and early social environments (Access pen or Control pen) for the non-binary variables: latency (unit: seconds), close distance (unit: percentage of time), explore pen fitting (unit: the number of times that explore pen fitting was observed) and explore floor (unit: the number of times that the behaviour of exploring the floor was observed).

	Genetic line		Early social environment	
	SY	DY	AP	CP
Item	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Latency (s)	21.3 ± 13.75	23.6 ± 15.60	24.2 ± 16.64	21.0 ± 12.51
Close distance (% of time)	0.7 ± 0.22	0.7 ± 0.23	0.7 ± 0.23	0.7 ± 0.23
Explore fitting (N times)	1.8 ± 1.35	1.3 ± 1.19	1.4 ± 1.21	1.7 ± 1.36
Explore floor (N times)	3.2 ± 1.51	3.5 ± 1.46	3.6 ± 1.40	3.1 ± 1.53

Abbreviations: SY = Swedish Yorkshire; DY = Dutch Yorkshire; AP = Access pen; CP = Control pen.

Table 4
Social interaction behaviours (binary variables) shown by the pigs under the paired interaction test (PIT) at 5 weeks divided over the genetic lines (Swedish Yorkshire and Dutch Yorkshire) and early social environments (Access pen and Control pen).

	5-week paired interaction test – binary variables			
	Genetic line		Early social environment	
	SY	DY	AP	CP
Unit	%	%	%	%
First interaction				
Meeting on focal gilt side	48.8	57.4	46.9	60.9
Focal gilt first	31.7	42.6	30.6	45.7
Activity				
Hop/spring	0.0	1.2	0.0	1.4
Scamper	18.7	16.0	15.0	19.6
Pivot	8.9	8.0	6.8	10.1
Toss head	0.0	3.1	2.0	1.4
Play at all	22.8	21.6	17.7	26.8
Social behaviour- performing				
Nosing body	67.5	72.2	69.4	71.0
Nibbling/biting	16.3	4.9	12.2	7.2
Climbing	4.9	0.6	3.4	1.4
Levering	4.1	2.5	2.7	3.6
Pushing	10.6	7.4	10.9	6.5
Social at all	75.6	75.3	73.5	77.5
Social more than once	45.5	38.3	38.8	44.2
Sound at all	37.4	27.2	28.6	34.8
Sound more than once	10.6	8.0	8.2	10.1
No sound	59.3	58.6	57.8	60.1
Grunt	35.8	27.2	27.2	34.8
Scream	2.4	0.0	2.0	0.0
Social behaviour receiving				
No reaction	51.2	46.3	49.7	47.1
Avoiding	17.9	16.7	14.3	20.3
Nosing body	25.2	30.9	28.6	28.3
Pushing	4.1	3.1	3.4	3.6
Nibbling/biting	6.5	7.4	7.5	6.5
Social at all	74.0	71.0	71.4	73.2
Social more than once	12.2	8.0	8.2	11.6
Sound at all	27.6	18.5	21.1	23.9
Sound more than once	9.8	6.8	4.8	11.6
No sound	65.0	65.4	64.6	65.9
Grunt	25.2	17.3	18.4	23.2
Scream	3.3	2.5	2.7	2.9

Abbreviations: SY = Swedish Yorkshire; DY = Dutch Yorkshire; AP = Access pen; CP = Control pen.

Table 5
Responses in the paired interaction test at 20 weeks of age for gilt of the genetic lines (Swedish Yorkshire or Dutch Yorkshire), early social environments (Access pen or Control pen) and late social environments (Mixed group or Intact group) for the non-binary variables: latency (unit: seconds), close distance (unit: percentage of time), explore pen fitting (unit: the number of times that explore pen fitting was observed) and explore floor (unit: the number of times that the behaviour of exploring the floor was observed).

	Genetic line		Early social environment		Late social environment	
	SY	DY	AP	CP	MG	IG
Item	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Latency (s)	11.8 ± 6.75	11.5 ± 6.60	11.5 ± 6.77	11.8 ± 6.57	11.8 ± 7.30	11.4 ± 6.06
Close distance (% of time)	0.7 ± 0.21	0.7 ± 0.29	0.7 ± 0.26	0.7 ± 0.26	0.7 ± 0.25	0.7 ± 0.27
Explore fitting (N times)	1.0 ± 1.10	1.4 ± 1.35	1.3 ± 1.27	1.2 ± 1.25	1.2 ± 1.25	1.3 ± 1.27
Explore floor (N times)	2.8 ± 1.87	3.4 ± 1.81	3.2 ± 1.85	3.2 ± 1.87	3.2 ± 1.86	3.2 ± 1.86

Abbreviations: SY = Swedish Yorkshire; DY = Dutch Yorkshire; AP = Access pen; CP = Control pen; MG = Mixed group; IG = Intact group.

tor play behaviour, and show increased activity and reactivity in social interactions during socially challenging paired interaction tests at both 5 and 20 weeks of age. The results showed that gilts with early social mixing experience were more likely to display locomotor play behaviour during the 20-week test than gilts in the control treatment, confirming that social experience can influence gilts' responses in this challenging scenario. Among the SY gilts, but not the DY gilts, experience of late social mixing meant that they were more likely to explore the pen floor during the 20-week test than gilts in the control treatment. Thus, the effects of genetic line on responses in the socially challenging paired interaction test were confirmed. Moreover, SY gilts explored the pen fittings more than DY gilts during 5-week test, as predicted. During the 20-week test, however, DY gilts explored the pen fittings more than SY gilts. During our observations, it was clear that social interactions of different types occurred during the social challenging tests (Tables 4 and 6). However, the occurrence of social behaviour was not clearly influenced by social experience or genetic line.

Table 6
Social interaction behaviours (binary variables) shown by the pigs under the paired interaction test (PIT) at 20 weeks divided over the genetic lines (Swedish Yorkshire and Dutch Yorkshire), early social environments (Access pen and Control pen) and late social environments (Mixed group or Intact group).

	20-week paired interaction test – binary variables					
	Genotype		Early social environment		Late social environment	
	SY	DY	AP	CP	IG	MG
Unit	%	%	%	%	%	%
First interaction						
Meeting on focal gilt side	41.5	56.6	70.8	28.3	44.0	56.8
Focal gilt first	26.8	26.4	20.8	32.6	29.4	24.4
Activity						
Hop/spring	4.9	10.7	11.6	4.4	10.9	5.2
Scamper	37.4	54.7	48.3	45.9	56.5	37.0
Pivot	13.0	15.7	15.6	13.3	13.6	15.6
Toss head	4.1	1.3	1.4	3.7	4.1	0.7
Play at all	45.5	59.7	57.1	49.6	61.9	44.4
Social behaviour- performing						
Nosing body	72.4	64.2	67.3	68.1	71.4	63.7
Nibbling/biting	22.8	13.8	19.7	15.6	21.1	14.1
Climbing	4.1	0.0	2.0	1.5	0.7	3.0
Levering	0.8	0.6	1.4	0.0	1.4	0.0
Pushing	4.1	3.1	2.0	5.2	2.7	4.4
Social at all	79.7	66.0	72.1	71.9	74.8	68.9
Social more than once	42.3	33.3	37.4	37.0	41.5	32.6
Sound at all	9.8	7.5	6.8	10.4	12.2	4.4
Sound more than once	2.4	0.6	1.4	1.5	2.7	0.0
No sound	78.0	62.9	68.7	70.4	71.4	67.4
Grunt	9.8	7.5	6.8	10.4	12.2	4.4
Scream	0.0	0.0	0.0	0.0	0.0	0.0
Social behaviour receiving						
No reaction	34.1	39.6	32.7	42.2	38.3	36.2
Avoiding	14.6	25.2	13.6	28.1	20.6	20.6
Nosing body	46.3	47.8	51.0	43.0	48.9	45.4
Pushing	3.3	1.9	2.0	3.0	2.8	2.1
Nibbling/biting	8.9	9.4	10.9	7.4	7.8	10.6
Social at all	54.5	62.9	57.8	60.7	60.3	58.2
Social more than once	19.5	23.3	19.0	24.4	22.0	21.3
Sound at all	7.3	6.3	8.2	5.2	5.0	8.5
Sound more than once	1.6	1.3	0.0	3.0	0.0	2.8
No sound	68.3	72.3	67.3	74.1	66.0	75.2
Grunt	5.7	5.0	8.2	2.2	5.0	5.7
Scream	1.6	2.5	1.4	3.0	0.0	4.3

Abbreviations: SY = Swedish Yorkshire; DY = Dutch Yorkshire; AP = Access pen; CP = Control pen; IG = Intact group; MG = Mixed group.

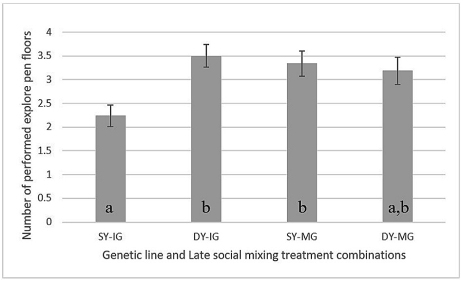


Fig. 5. Number of 'explore floor' events performed by the focal gilts per treatment (genetic line: Swedish Yorkshire (SY) or Dutch Yorkshire (DY) and late social mixing environment: Mixed group (MG) or Intact group (IG)) combinations in the paired interaction test at 20 weeks of age (PIT20w) (Least Square Means ± SE). Different letters (a,b) for different observation minutes indicate pair-wise differences at $P < 0.05$.

Effects of social treatments

Overall, the social mixing experience had minor effects on the gilt's behavioural responses in the PITs. Behaviours indicating negative social behaviours were very low, and instead, the effects related to the positive welfare indicator of play behaviours were observed. Play is a cognitively demanding activity which reduces attentiveness to external threats, so play behaviour generally occurs when animals perceive their situation as safe (Špinka et al., 2001). In this study, we expected gilts with extra social experience (AP and/or MG) to exhibit more locomotor play behaviour, as their greater exposure to complex situations might make them perceive the situation as safer compared to gilts with less social experience (CP and/or IG). Although extra pre-weaning social experience had no effect on locomotor play behaviour at the 5-week test, it did lead to more locomotor play behaviour by the 20-week test. This suggests that gilts with additional pre-weaning social experience (AP/MG) may have developed better social skills and perceived the test situation as relatively safe, or at least less negative, compared to gilts with less social experience. This is in line with previous findings that early socialised animals have higher behavioural plasticity (Edwards and Telkänranta, 2024) and occurred despite no prior habituation to the arena. The extra socialisation pre-weaning perhaps provided an additional level of complexity to the social environment (Edwards and Telkänranta, 2024) in the early development of AP/MG gilts, since besides the early social experience, they also experienced a change of environment.

Effects of genetic line

Social ability is not included as a breeding trait in modern pig breeding and is thus not directly selected for, but sow lines have been indirectly selected for social behaviours favourable for the environment in which they were evaluated and selected. The SY line has been evaluated and selected in group housing systems since the 1980 s, while in the same period, the DY line has been indirectly selected for social behaviours favourable for individually stalled systems. Therefore, we expected gilts of the SY line to display more social behaviour and be more alert to their surroundings than gilts of the DY line. But, in contrast to previous findings of indirect genetic effects on aggressive behaviour (Canario et al., 2012; Camerlink et al., 2013), we observed no differences in social behaviour between the genetic lines. Interestingly, gilts from the SY line spent more time in close proximity to the opponent gilt during the 20-week test, indicating perhaps that they sought social support in the new and unknown environment. However, as there were no differences in social interactions between the genetic lines, this finding should be interpreted with caution.

We also expected gilts of the SY line to explore their surroundings more, because the SY line has been selected to thrive in a more complex group housing social environment than gilts of the DY line. We found that SY gilts explored the pen fittings more in the 5-week test, but not in the 20-week test (where DY gilts showed more exploration behaviour than SY gilts). SY gilts with the late social mixing environment of IG also showed less exploration of the floor during the 20-week test. In a novel situation and arena, exploration of the pen interior may indicate that the pig is not startled and is calm enough to show interest in the surrounding environment.

Changes in behaviour over time

Even though the social challenging test was only 3 min long, changes in behaviour during the test were observed in both the 5- and 20-week tests. In the 5-week test, gilts spent less time in close proximity during the first minute of the test and they explored the pen fittings more in the last minute. They also showed an increase in avoidance of social interactions when approached by the other individual over time in the test. In the 20-week test, gilts expressed most locomotor play during the first minute, spent more time close to one another during the second minute and spent more time exploring both floor and fittings of the test arena during the last minute of the test. These appear to be logical changes in behaviour over time in the test, with initial excitement in the novel area, resulting in locomotor play (Rauw, 2013, Horback, 2014), and thereafter increased interest in the other pig and the pen fittings and floor.

Previous studies have shown that additional social experience gained from meeting new individuals during the suckling period improves piglets' social skills and reduces the duration of aggression (e.g. D'Eath, 2005; Salazar et al., 2018; Morgan et al., 2014; Martin et al., 2015). However, all those studies were carried out in conventional crated systems or in experimental settings. In the present study, commercial loose housing pens were used. Furthermore, in previous studies of co-mingling, the test piglets have been intended for slaughter rather than as breeding sows in piglet production. As loose housing of farrowing sows is becoming the new standard in the EU and may be mandatory if the proposed ban on sow crates is introduced (European Union, 2023), additional investigations into loose housing systems are required.

Ethics approval

The experiment and all procedures involved were approved by the National Ethics Committee for Animal Experiments in Uppsala (Registration number: 5.8.18-16279/2017).

Data and model availability statement

None of the data have been deposited in an official repository. The data that support the study findings are available from the authors upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

Author ORCIDs

Linda Marie Backeman Hannius: https://orcid.org/0000-0003-1533-9966.

Linda Keeling: https://orcid.org/0000-0003-2629-0117.

Daiana de Oliveira: https://orcid.org/0000-0002-6787-2626.

Claes Anderson: https://orcid.org/0009-0005-0789-4195.

Anna Wallenbeck: https://orcid.org/0000-0001-8012-2849.

CRediT authorship contribution statement

L.M. Backeman Hannius: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **L. Keeling:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **D. de Oliveira:** Writing – review & editing, Methodology, Conceptualization. **C. Anderson:** Writing – review & editing, Methodology, Conceptualization. **A. Wallenbeck:** Writing – review & editing, Supervision, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of interest

None.

Acknowledgements

The authors thank the staff at Swedish Livestock Research Centre (Lövsta) pig research facilities for their support during the study, and Stina Emriksson for help with the documentation of behaviours from the video recordings.

Financial support statement

This research was funded by FORMAS, reference number: 2016-01787.

References

Bieber, C., Rauchenschwandtner, E., Michel, V., Suchentrunk, F., Smith, S., Vetter, S. G., 2019. Forming a group in the absence of adult females? social networks in yearling wild boars. Applied Animal Behaviour Science 217, 21–27.

Camerlink, I., Turner, S.P., Bijma, P., Bolhuis, J.E., 2013. Indirect genetic effects and housing conditions in relation to aggressive behaviour in pigs. PLoS ONE 8, 1–9.

Camerlink, I., Turner, S.P., Farish, M., Arnott, G., 2015. Aggressiveness as a component of fighting ability in pigs using a game-theoretical framework. Animal Behaviour 108, 183–191.

Camerlink, I., Turner, S.P., Farish, M., Arnott, G., 2019. Advantages of social skills for contest resolution. Royal Society Open Science 6, 181456.

Canario, L., Turner, S.P., Roehe, R., Lundeheim, N., D'Eath, R.B., Lawrence, A.B., Knol, E., Bergsma, R., Rydhmer, L., 2012. Genetic associations between behavioral traits and direct-social effects of growth rate in pigs. Journal of Animal Science 90, 4706–4715.

Colson, V., Martin, E., Orgeur, P., Prunier, A., 2012. Influence of housing and social changes on growth, behaviour and cortisol in piglets at weaning. Physiology & Behavior 107, 59–64.

Coutellier, L., Arnould, C., Boissy, A., Orgeur, P., Prunier, A., Veissier, I., Meunier-Salaün, M.C., 2007. Pig's responses to repeated social regrouping and relocation during the growing-finishing period. Applied Animal Behaviour Science 105, 102–114.

D'Eath, R.B., 2004. Consistency of aggressive temperament in domestic pigs: The effects of social experience and social disruption. Aggressive Behavior 30, 435–448.

D'Eath, R.B., 2005. Socialising piglets before weaning improves social hierarchy formation when pigs are mixed post-weaning. Applied Animal Behaviour Science 93, 199–211.

D'Eath, R.B., Pickup, H.E., 2002. Behaviour of Young Growing Pigs in a Resident-Intruder Test Designed to Measure Aggressiveness. Aggressive Behavior 28, 401–415.

D'Eath, R.B., Turner, S., 2009. The natural behaviour of the pig. In: Marchant-Forde, J. (Ed.), The Welfare of Pigs. Springer Science, Dordrecht, The Netherlands, pp. 13–45.

De Leeuw, J.A., Ekkel, E.D., 2004. Effects of feeding level and the presence of a foraging substrate on the behaviour and stress physiological response of individually housed gilts. Applied Animal Behaviour Science 86, 15–25.

Dingemanse, N.J., Wolf, M., 2013. Between-individual differences in behavioural plasticity within populations: Causes and consequences. Animal Behaviour 85, 1031–1039.

Edwards, S.A., Telkänranta, H., 2024. 11 - Lifetime consequences of the early physical and social environment of piglets. In: Camerlink, I., Baxter, E.M. (Eds.), Advances in Pig Welfare. Second Ed. Woodhead Publishing, Cambridge, UK, pp. 241–260.

Emriksson, S.,2021. Short-term effects of early social experiences on reactions to unfamiliar pigs. Master thesis, Swedish University of Agricultural Sciences (SLU), Department of Animal Environment and Health, Uppsala, Sweden.

European Union, 2023, End the Cage Age. Retrieved on 18 December 2023, from: https://citizens-initiative.europa.eu/initiatives/details/2018/000004/end-cage-age_en.

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution 7, 1325–1330.

Goumon, S., Illmann, G., Leszkowová, I., Dostalová, A., Cantor, M., 2020. Dyadic affiliative preferences in a stable group of domestic pigs. Applied Animal Behaviour Science 230, 105045.

Hannius, LM., 2019. Difference in general behaviour and social interactions of young Yorkshire gilts in different social environments. Master thesis, Swedish University of Agricultural Sciences (SLU), Department of Animal Environment and Health, Uppsala, Sweden.

Held, S.D.E., Špinka, M., 2011. Animal play and animal welfare. Animal Behaviour 81, 891–899.

Horback, K., 2014. Nosing around: play in pigs. Animal Behavior and Cognition 2, 186.

Jensen, P., 1986. Observations on the maternal behaviour of free-ranging domestic pigs. Applied Animal Behaviour Science 16, 131–142.

Kaminski, G., Brandt, S., Baubet, E., Baudoin, C., 2005. Life-history patterns in female wild boars (Sus scrofa): mother–daughter postweaning associations. Canadian Journal of Zoology 83, 474–480.

Kanaan, V.T., Lay, D.C., Richert, B.T., Pajor, E.A., 2012. Increasing the frequency of Co-mingling piglets during the lactation period alters the development of social behavior before and after weaning. Journal of Applied Animal Welfare Science 15, 163–180.

Koolhaas, J.M., Coppens, C.M., de Boer, S.F., Buwalda, B., Meerlo, P., Timmermans, P.J. A., 2013. The resident-intruder paradigm: A standardized test for aggression, violence and social stress. Journal of Visualized Experiments 77, 4367.

Lawrence, A., 1987. Consumer demand theory and the assessment of animal welfare. Animal Behaviour 35, 293–295.

Lenth, R.V., Buerkner, P., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H. & Singmann, H., 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means. Retrieved on 4 October 2022, from: https://cran.r-project.org/package=emmeans.

Martin, J.E., Ison, S.H., Baxter, E.M., 2015. The influence of neonatal environment on piglet play behaviour and post-weaning social and cognitive development. Applied Animal Behaviour Science 163, 69–79.

Morgan, T., Pluske, J., Miller, D., Collins, T., Barnes, A.L., Wemelsfelder, F., Fleming, P. A., 2014. Socialising piglets in lactation positively affects their post-weaning behaviour. Applied Animal Behaviour Science 158, 23–33.

Nihlstrand, J. 2016. Chicory and red clover silage to growing/finishing pigs and its influence on pigs' behaviour. Master thesis, Swedish University of Agricultural Sciences (SLU), Department of Animal Breeding and Genetics, Uppsala, Sweden.

Oldham, L., Camerlink, I., Arnott, G., Doeschl-Wilson, A., Farish, M., Turner, S.P., 2020. Winner–loser effects overrule aggressiveness during the early stages of contests between pigs. Scientific Reports 10, 13338.

Peden, R.S.E., Turner, S.P., Boyle, L.A., Camerlink, I., 2018. The translation of animal welfare research into practice: the case of mixing aggression between pigs. Applied Animal Behaviour Science 204, 1–9.

Petersen, H.V., Vestergaard, K., Jensen, P., 1989. Integration of piglets into social groups of free-ranging domestic pigs. Applied Animal Behaviour Science 23, 223–236.

Podgórski, T., Lusseau, D., Scandura, M., Sönnichsen, L., Jędrzejewska, B., 2014. Long-lasting, kin-directed female interactions in a spatially structured wild boar social network. PLOS ONE 9, e99875.

Poteaux, C., Baubet, E., Kaminski, G., Brandt, S., Dobson, F.S., Baudoin, C., 2009. Socio-genetic structure and mating system of a wild boar population. Journal of Zoology 278, 116–125.

Quality, W., 2009. Welfare Quality ® Assessment protocol for pigs (sows and piglets, growing and finishing pigs). Welfare Quality Consortium, Lelystad, The Netherlands.

R Core Team., 2021. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R: The R Stats Package, 2021. The R Stats Package. Retrieved on 4 October 2022, from: https://stat.ethz.ch/R-manual/R-devel/library/stats/html/00Index.html.

Rauw, W.M., 2013. A note on the consistency of a behavioral play marker in piglets. Journal of Animal Science and Biotechnology 4, 1–7.

Rydhmer, L., 2021. Advances in understanding the genetics of pig behaviour. Burleigh Dodds Series in Agricultural Science, Cambridge, UK.

Salazar, L.C., Ko, H.L., Yang, C.H., Llonch, L., Manteca, X., Camerlink, I., Llonch, P., 2018. Early socialisation as a strategy to increase piglets' social skills in intensive farming conditions. Applied Animal Behaviour Science 206, 25–31.

Špinka, M., Newberry, R.C., Bekoff, M., 2001. Mammalian play: training for the unexpected. Quarterly Review of Biology 76, 141–168.

Stolba, A., Wood-Gush, D.G.M., 1989. The behaviour of pigs in a semi-natural environment. Animal Production 48, 419–425.

Taborsky, B., 2021. A positive feedback loop between sociality and social competence. Ethology 127, 774–789.

Turner, S.P., Nevison, I.M., Desire, S., Camerlink, I., Roehe, R., Ison, S.H., Farish, M., Jack, M.C., D'Eath, R.B., 2017. Aggressive behaviour at regrouping is a poor predictor of chronic aggression in stable social groups. Applied Animal Behaviour Science 191, 98–106.

Turner, S.P., Weller, J.E., Camerlink, I., Arnott, G., Choi, T., Doeschl-Wilson, A., Farish, M., Foister, S., 2020. Play fighting social networks do not predict injuries from later aggression. Scientific Reports 10, 15486.

Vahlberg, J., 2019. Difference in health and behaviour between two different pig line crosses. Master thesis, Swedish University of Agricultural Sciences (SLU), Department of Animal Breeding and Genetics, Uppsala, Sweden.

Varela, S.A.M., Teles, M.C., Oliveira, R.F., 2020. The correlated evolution of social competence and social cognition. Functional Ecology 34, 332–343.

Weller, J.E., Camerlink, I., Turner, S.P., Farish, M., Arnott, G., 2019. Socialisation and its effect on play behaviour and aggression in the domestic pig (Sus scrofa). Scientific Reports 9, 4180.

Xin, H., DeShazer, J.A., Leger, D.W., 1989. Pig vocalizations under selected husbandry practices. Transactions of the American Society of Agricultural Engineers 32, 2181–2184.

III

frontiers | Frontiers in Animal Science

TYPE Original Research
PUBLISHED 10 December 2025
DOI 10.3389/fanim.2025.1711609

Check for updates

OPEN ACCESS

EDITED BY
Jeremy N. Marchant,
Organic Plus Trust Inc., United States

REVIEWED BY
Andrea Luttman,
Michigan State University, United States
Leandro Sabei,
University of São Paulo, Brazil

*CORRESPONDENCE
Linda Marie Backeman Hannius
linda.marie.hannius@slu.se

RECEIVED 23 September 2025
REVISED 06 November 2025
ACCEPTED 13 November 2025
PUBLISHED 10 December 2025

CITATION
Backeman Hannius LM, Keeling L and Wallenbeck A (2025) Under pressure: effect of first-parity sows' early social experience and genetic line on behavior and lesions in a paired interaction test with an older sow. *Front. Anim. Sci.* 6:1711609.
doi: 10.3389/fanim.2025.1711609

Under pressure: effect of first-parity sows' early social experience and genetic line on behavior and lesions in a paired interaction test with an older sow

Linda Marie Backeman Hannius*, Linda Keeling and Anna Wallenbeck

Department of Applied Animal Science and Welfare, Swedish University of Agricultural Sciences, Uppsala, Sweden

Sows housed in groups navigate complex social relationships, and individual differences affect their engagement and stress responses. To explore what shapes these differences, this study examined how genetic background and early-life social experiences affect social behavior, response strategies, and risk of injury among young sows during pairwise social interactions with unfamiliar older sows. 79 first-parity sows of two genetic lines, Swedish Yorkshire and Dutch Yorkshire, were raised in either socially mixed litters (with access to non-littermates through shared piglet areas) or conventional pens. At 10 weeks, they were either grouped with unfamiliar gilts or remained with their original littermates. After first weaning, each sow was introduced to an unfamiliar older sow in a 60-min interaction test, with behaviors recorded and lesions assessed before and after. By coding both the initiator's behavior and the response, and linking these to lesion placement, more nuanced response patterns could be analyzed for the short-term development of agonistic encounters. Swedish Yorkshire sows exhibited more aggression, responded more forcefully, and sustained more injuries, particularly to the front and rear of the body, compared to Dutch Yorkshire sows, which showed less aggression and fewer lesions. Early-life social mixing correlated with more affiliative behaviors and a tendency not to react in social interactions, suggesting greater social tolerance, though not reduced injury risk. Social mixing later in rearing was not associated with behavior or lesion counts. Interaction effects were sparse, indicating broadly similar behavior–lesion associations across genetic lines and rearing treatments in this paired interaction test with two sows. A few behavior-specific associations were observed, such as a higher lesion risk among late-mixed sows showing defensive responses, but these were limited in scope and not consistent across outcomes. Across treatments and lines, retreat was common among first-parity sows, which may offer short-term protection but could have longer-term costs in social learning and affiliation. While the controlled test setting allowed for precise measurement of social tendencies, real-world group housing involves more complex interactions. These findings highlight the need to consider genetic line and early experience when evaluating social behavior and indicate that future studies should assess these effects under practical group housing conditions.

KEYWORDS

damaging behavior, social mixing, injuries, genetic selection, animal welfare assessment, group housing, pigs, gilts

1 Introduction

It is widely known that intensive pig production can compromise animal welfare (Albernaz-Gonçalves et al., 2021). While it is challenging to completely eliminate stressors in commercial farming systems, changes to improve pig welfare have been suggested within, e.g., the European Union (EU) (Council of the European Union, 2008), the United States (McGlone, 2013), and New Zealand (Weaver and Morris, 2004), in line with increased public concern about animal welfare (European Commission, 2023). Within the EU, public concern has resulted in initiatives such as the more recent "End the Cage" campaign. Earlier examples of policy changes include the EU ban on individual stalls for sows during part of their pregnancy, which came into force on 1 January 2013 (Council of the European Union, 2008). In Sweden, there is extensive experience with housing dry sows in groups, as confinement of dry sows has been prohibited since 1988 (Djurskyddsförordning (1988:539), 1988; Djurskyddsförordning (2019:66), 2019).

Group housing of sows has been studied extensively, and there is consensus that this practice enhances sow welfare (Verdon et al., 2015; Maes et al., 2016; Sylvén et al., 2025). Well-managed group housing systems are associated with improved opportunities for species-specific behaviors, including social behaviors, and reduced stereotypies (Scientific Veterinary Committee, 1997; Chapinal et al., 2010). However, group housing also introduces certain disadvantages, as sows must be regrouped (Razdan, 2003; Gonyou, 2005). Regrouping can lead to increased aggression among sows as new social hierarchies are established (Greenwood et al., 2014). Aggressive interactions between sows follow similar patterns to those observed in wild boars (Jensen, 1986) and involve contact behaviors such as biting and pushing, as well as non-contact intimidation through body postures and threats (McGlone, 1985). Threats and even mere visual contact can cause stress in low-ranking animals (Boyle et al., 2012). Older sows are generally more dominant than younger sows and more frequently engage in aggressive encounters at mixing (Strawford et al., 2008). The welfare issues associated with group housing arise either directly from the stress and lesions caused by aggression or indirectly through problems such as lameness (Boyle et al., 2012). Lesions caused by aggression are typically cuts or scratches on the skin (Maes et al., 2016). Injuries resulting from aggression can impair reproductive performance and contribute to the culling of sows, especially early-parity sows (Engblom et al., 2007), which increases costs (Stalder et al., 2007). Hence, aggression poses a serious threat not only to sow welfare but also to herd economics (Barnett et al., 2001; Marchant-Forde, 2010; Greenwood et al., 2014). This emphasizes the need to develop management practices for group housing systems that reduce welfare risks, particularly for young sows, and thus reduce economic losses for farmers.

The behavioral repertoire of domestic pigs remains relatively similar to that of their wild counterparts (Stolba and Wood-Gush, 1989; D'Eath and Turner, 2010; Goumon et al., 2020) despite domestication and selective breeding. However, artificial selection for production traits and adaptation to different housing environments have shaped how pigs interact (Rydhmer, 2021). For example, dam-lines have been selected for performance under either individual stalls or group housing systems, which may have indirectly influenced traits linked to social tolerance, aggression control, and conflict resolution. In Sweden, the Swedish Yorkshire (SY) line has been selected under group-housing conditions since the 1980s, whereas the Dutch Yorkshire (DY) line was developed under stall-based systems until the early 2020s. These divergent selection histories may therefore have led to differences in social competence and adaptability between these genetic lines when housed in groups.

Under commercial production conditions, piglets generally have limited opportunities to interact with non-littermates before weaning. This restricted social environment may hinder the development of social competence and increase the risk of stress and aggression when pigs encounter unfamiliar conspecifics post-weaning (Coutellier et al., 2007; Colson et al., 2012; Turner et al., 2017). Allowing early-life social contact between adjacent litters, often referred to as co-mingling, has been studied over the past decade due to its potential to enhance piglets' social competence and decrease aggressive interactions (Wattanakul et al., 1997; Hessel et al., 2006; Morgan et al., 2014; Camerlink et al., 2018; Salazar et al., 2018). Early socialization has been shown to modify later social responses: socialized piglets display faster but less intense agonistic interactions and form hierarchies more efficiently (D'Eath, 2005; Kanaan et al., 2012; Camerlink et al., 2018; Camerlink et al., 2019; Weller et al., 2019; Oldham et al., 2020). They also show greater behavioral flexibility and more appropriate social responses (Weller et al., 2019), a trait described as social ability, defined as the capacity to adjust social behavior to environmental and social demands (Varela et al., 2020; Taborsky, 2021). Social ability is a multifactorial trait influenced by genetics, early experiences, and social contexts (Dingemanse and Wolf, 2013).

While earlier co-mingling studies provide valuable insights into the short-term benefits of early socialization, they differ from the approach applied in the present work. In most previous studies, piglets were fully mixed during lactation while their dams were confined in farrowing crates, limiting sow–piglet interactions and removing potential influences of maternal behavior and group-housing factors. Moreover, previous research has primarily focused on piglets or growing pigs, whereas little is known about whether the effects of early social experiences persist into adulthood and influence social behavior in reproductive sows. The present study therefore extends this line of research by examining pigs that experienced controlled inter-litter contact during the nursing period and later evaluating them as first-parity sows in a social challenge test, linking early management conditions to later social competence in a group-housing context.

Evaluating social competence in pigs can be challenging, as it requires distinguishing between immediate aggressive responses and broader behavioral tendencies. Standardized behavioral tests, such as paired-interaction or resident–intruder tests, provide a structured framework to assess individual responses under controlled conditions (D'Eath and Pickup, 2002; D'Eath, 2004; Koolhaas et al., 2013; Camerlink et al., 2015; Turner et al., 2020; Backeman Hannius et al., 2024). These tests allow systematic evaluation of both social and exploratory behaviors, offering insight into how early-life experiences may shape later social functioning.

The aim of this study was to assess the effects of genetic line and social mixing experiences during early life on social and damaging behaviors, lesions, and the associations between behaviors and lesions in first-parity sows (FPSs) during a paired-interaction test with an older sow. Testing was carried out after weaning the young sows' first litter, at a time when they would normally be introduced to an established group of sows. We hypothesized that FPSs with extra social mixing experience and of the Swedish Yorkshire line would have fewer wounds and exhibit fewer behaviors associated with injury compared to FPSs without extra social mixing experience and of the Dutch Yorkshire line.

2 Materials and methods

The experiment and all procedures were approved by the National Ethics Committee for Animal Experiments in Uppsala (registration number: 5.8.18-16279/2017). The experiment was performed at the Swedish Livestock Research Centre, Lövsta, Uppsala, Sweden, from 2018 to 2020.

2.1 Animals, housing, and management

This study included 79 first-parity sows (FPSs) from two genetic lines: purebred Swedish Yorkshire (SY) and at least 75% Dutch Yorkshire (DY). The sows originated from 26 litters divided into seven batches. The first batch was born in January 2018, and the last in November of the same year. Litters were housed in loose-housed farrowing pens from birth until 10 weeks of age and were weaned at 34.0 ± 1.82 days. The average weight was 1.58 ± 0.27 kg at birth and 11.8 ± 2.01 kg at weaning.

This study was part of a larger research project. A detailed description of housing conditions and experiences up to 20 weeks of age is provided elsewhere (Backeman Hannius et al., 2024). In the earlier study (Backeman Hannius et al., 2024), the focus was on short-term effects of social mixing and genetic line on young gilts' social and exploratory responses in three-minute standardized interaction tests. The present study examined the long-term effects of social mixing and genetic line, and thus animals were assessed over an extended period. Between the two studies, 17 FPSs were excluded [79 FPSs included in this study compared to 96 gilts in the previous study (Backeman Hannius et al., 2024)) due to failure to conceive or fetal loss (N = 8), health issues leading to culling (N = 7), farrowing before transfer to the designated pen (N = 1), and exclusion after a sow broke the door to the test arena at the start of testing (N = 1). These exclusions ensured consistency throughout the study.

The FPSs were kept and handled according to Swedish regulations during all production stages. In summary, housing conditions during the first 20 weeks of life according to Swedish pig production standards are characterized by loose-housed farrowing pens, no tail docking, and routine provision of straw as manipulable enrichment. At 10 weeks of age, the future FPSs were moved to a growing stable in groups of four gilts, where they were housed until 20 weeks of age (see (Backeman Hannius et al., 2024) for details). At 20 weeks of age, they were moved to the sow barn of the research facility.

Within the sow barn, four types of pens were relevant to this study: gilt recruitment pens, non-pregnant gilt pens, breeding pens, and pregnant gilt pens. The future FPSs were initially moved as a group of four to gilt recruitment pens (total size: 7.2 m × 4.5 m), consisting of a deep-litter bedding area (5.0 m × 4.5 m) and an elevated concrete area (2.2 m × 4.5 m) with gilt-sized self-closing feeding stalls. Gilts (and later sows) always had ad libitum access to water via at least one drinking nipple, positioned in the corner of the deep-straw bedding.

They remained in gilt recruitment pens until reaching approximately 80 kg (approximately 26 weeks of age), after which they were transferred to non-pregnant gilt pens. These pens were the same size and had a similar design as the gilt recruitment pen, containing a deep litter bedding area and an elevated concrete section with larger feeding stalls. The FPSs were inseminated while in these pens at 7–8 months of age, depending on their estrous cycle (earliest at second estrus) and on how many gilts could be integrated into the matching sow group after weaning their first litter. Between 3 and 4 weeks after insemination, the FPSs were transferred with their gilt group to the pregnant gilt pens, where they remained until moved to an individual farrowing pen approximately 1 week before the expected farrowing date.

The pregnant gilt pens were half the size (7.2 m × 2.25 m) of the non-pregnant gilt pens. The loose-housed farrowing pens (total size: 3.35 m × 2.0 m) consisted of a concrete lying and feeding area (2.1 m × 2.0 m), a slatted dunging area (1.25 m × 2.0 m), and a concrete-floored piglet corner with a roof, heat lamp, and floor heating accessible only to piglets.

A summary of the experimental design is presented in Figure 1.

The farrowing pens were manually cleaned every morning. Two days before the estimated farrowing date, each pen was provided with approximately 15–20 kg of chopped straw. Due to the slatted floor, the straw gradually decreased, and additional straw was added as needed, following standard Swedish practice. The FPSs were fed a standard commercial dry feed for lactating sows twice daily until 10 days after farrowing. Thereafter, they were fed three times daily until weaning, and piglets had access to creep feed. Each FPS and her piglets had ad libitum access to water from two drinking nipples placed 0.10 m and 0.15 m above the slatted floor.

2.2 Social mixing environments

2.2.1 Early social mixing environments

Each farrowing batch contained four sows with litters included in the study. Two were assigned to the control treatment, and two were assigned to the early social mixing environment. In the pens designated for early social mixing, a pop-hole (0.35 m × 0.30 m) was installed in the piglet corner between two side-by-side pens (Figure 2).

The pens with the pop-hole were designated access pens (APs). The APs allowed piglets to move freely and co-mingle between the two pens but prevented the sows from accessing the neighboring pen. This created an extended social environment for piglets in the AP treatment. The pop-hole was opened when AP piglets were 2 weeks old (13.1 ± 1.79 days), aligning with the natural socialization period when piglets in feral groups would interact with unfamiliar piglets (Jensen, 1986). Thus, it simulated a more natural early social mixing environment within a conventional housing system. The pop-hole was closed at weaning when piglets were approximately 5 weeks old (34.3 ± 1.87 days). The remaining two pens in each batch lacked a pop-hole, giving them the designation closed pens (CPs), and were used as the control treatment. The study design was balanced with two APs and two CPs in each batch, as well as two pens designated for each genetic line (DY and SY). This ensured that piglets in the AP treatment were exposed to piglets from the other genetic line. However, due to a shortage of SY litters, two of the 13 litters in the AP treatment did not co-mingle with any litters of the other genetic line. In one batch, two DY litters were mixed, and in another batch, a DY litter was paired with a crossbred (SY × DY) litter. Piglets of the SY × DY line were excluded from the analysis.

2.2.2 Late social mixing environment

When the FPSs reached approximately 10 weeks of age (67.9 ± 7.66 days), they were transferred to an experimental growing pig stable. Here, the new FPS groups of four were housed in pens (total area: 3.96 m × 1.80 m) with a concrete-floored area for feeding and lying, alongside a slatted dunging section measuring 1.80 m × 1.00 m. The slatted dunging section was elevated 0.18 m above the concrete floor of the pen.

In the late social mixing environment, two out of the four future FPS groups from each batch were placed in a mixed group (MG), and the other two groups were placed in an intact group (IG). In the IG, the future FPSs were housed with individuals from their own litter, with whom they had already established social bonds. In contrast, the MG FPSs from two different litters were combined, with each group containing one familiar FPS and two unfamiliar ones, which required the FPSs to interact with unknown individuals. The FPSs remained in these groups until they were transferred to individual farrowing pens 1 week before the expected farrowing.

This experimental setup resulted in four social-experience combinations balanced across genetic lines (Table 1).

2.3 Paired interaction test after weaning FPSs first litter

The paired interaction test (PIT) between the FPS and an older sow occurred on the day of weaning. For the FPSs, weaning of their

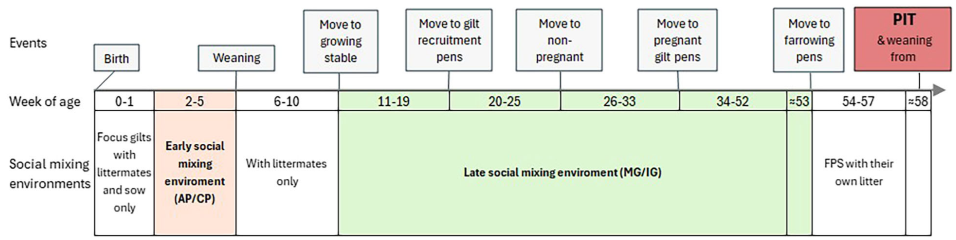


FIGURE 1
Experimental timeline from birth to the PIT performed after weaning of the first litter. Events above the axis mark key management events (birth, weaning, transfers to growing stable, gilt-recruitment stable, non-pregnant gilt pens and pregnant gilt pens and farrowing). Colored bands below the axis indicate the social-mixing treatments applied at each stage: early social mixing (AP, access pen or CP, closed pen) and late social mixing (MG= mixed group or IG, intact group).

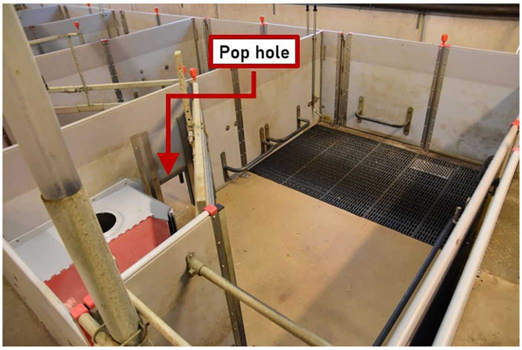


FIGURE 2
Picture of the right-hand pen of two access pens (APs), created from conventional loose housing farrowing pens, with a pop hole situated between the piglet corners in each pen. The image is reused from from Backeman Hannius et al. (2024), Animal 18:101349, under the CC BY 4.0 license.

first litter occurred at approximately 58 weeks of age (408.9 ± 26.03 days). In the days leading up to the PIT, a research assistant identified suitable older sows within the sow group into which each FPS would be integrated after weaning. Preference was given to older sows (at least second parity) that were entirely unrelated to the study, i.e., not dams of FPSs, not FPSs from previous batches, and not sows that had previously acted as opponents (N = 50).

Of the available sows, an older sow was randomly selected to be paired with an FPS for the PIT to avoid bias. If such sows were unavailable, priority was given to older sows that had previously served as opponents in a PIT (N = 27). As a last resort, sows originally investigated as FPSs that had completed the experiment and were no longer part of the study were selected (N = 2). Although it was not always possible to use an older sow completely independent of the study, all pairs consisted of an older opponent sow and an FPS that had never encountered each other.

The PIT was performed in the sow group housing pen (total size: 7.00 m × 7.20 m), designated the test arena, where the FPS would later be integrated. The test arena (Figure 3) included the deep-straw bedding section of the pen (5.00 m × 7.00 m). The feeding area occupying the remainder of the pen was locked and inaccessible. A drinking nipple was available in the corner of the test arena, and a large rectangular straw bale (2.30 m × 0.85 m × 0.90 m) was placed in the center. All sows around the test arena that could potentially interact with the test animals were moved. Before the test commenced, both sows were marked with a pattern for individual identification.

The PIT always started with the younger sow being removed from her farrowing pen, guided to the sow barn, and subsequently led into the test arena. After this, the older sow was brought from her farrowing pen to the sow barn and guided into the test arena. Once the older sow entered, the gate of the arena was closed, and the sows were allowed to interact for 60 min. A research assistant monitored the test via live video on screens placed in a separate area from the test pen to intervene if necessary, i.e., if the endpoint specified in the ethical permit was reached. This endpoint was defined as the onset of unresponsiveness, evident apathy, or physical impairment preventing the sow from adequately reacting to or escaping social contact. In practice, none of the animals reached these predefined endpoints, and thus no intervention was required.

TABLE 1 Frequencies of first parity sows (FPSs) allocated to each combination of early and late social experience, presented separately for the two genetic lines.

Early social experience	Late social experience	SY gilts	DY gilts	Total gilts
AP (Yes)	MG (Yes)	11	11	22
AP (Yes)	IG (No)	5	11	16
CP (No)	MG (Yes)	10	6	16
CP (No)	IG (No)	11	14	25
Total		38	43	79

Rows represent combinations of early social mixing (AP, access pen; CP, closed pen and late social environment after weaning (MG, mixed group; IG, intact group)), where AP and MG involve social experience (Yes) and CP and IG do not involve social mixing (No). Columns indicate the genetic line of the FPS (SY, Swedish Yorkshire; DY, Dutch Yorkshire. Frequencies denote the number of FPSs) assigned to each social experience × genetic line combination.

FIGURE 3
The test arena for pigs in the paired interaction test (PIT) carried out after weaning of the first parity sow's (FPS's) litter.

After 60 minutes, the feeding stalls were opened, and once the sows entered them, they were locked in. The sows were then individually guided to separate holding pens, where they remained until all pairs from that testing session had been evaluated. Following this, both the FPSs and older sows were integrated into their designated sow group according to standard procedures of the research herd.

2.4 Data collection

2.4.1 Behavioral observations

Behavioral observations were made from video recordings of each PIT pair. The cameras were elevated, attached to stable fixtures on opposite sides of the test arena, to cover the entire arena from two angles. The observation period began when the older sow's front legs entered the deep-bedded area, and behavior was continuously observed.

An ethogram (Table 2) was used to register the social behavior of the performing sow, the response of the receiver sow, the targeted body part of the interaction (if physical contact occurred), other social behaviors, time, and which sow initiated the first interaction. A behavioral change or a pause lasting at least three seconds was used as the criterion for recording a new behavior. The recordings from each PIT pair were analyzed using BORIS event-logging software (version 7.9.8 [Friard and Gamba, 2016)].

The ethogram was developed based on and refined from previous studies (e.g., Jensen, 1980; Weng et al., 1998; Rault, 2017) and further adjusted through a pilot study. The pilot study involved eight randomly selected PITs, each continuously observed for the full 60-min duration by a trained observer. The analysis showed that most social behaviors occurred within the first 20 min, while the final 10 min provided additional behavioral information. Considering the substantial time required to analyze full-length video recordings, a key objective was to reduce the observation period without compromising data quality. Therefore, behavioral data were collected for minutes 1–20 and minutes 50–60 of the test for all FPSs in the final dataset. All behavioral observations were conducted by a single trained research assistant to ensure consistency.

2.4.2 Lameness and lesions

Lameness and skin lesions were assessed before and after each PIT on the FPSs but not on the older sows. Approximately 30 min before the first test started, all FPSs from the batch were assessed to establish individual baselines. The health assessment was based on the Welfare Quality® protocol (Welfare Quality, 2009) and included evaluations of lameness and injuries. Lameness was categorized as: no remarks (normal gait); slight lameness (the animal has difficulty walking but is still using all legs); or severe lameness (the animal is severely lame, is putting minimal or no weight on the affected limb, or is unable to walk).

Skin lesions were examined on the ears, front, midsection (middle), hindquarters, legs, and tail (Figure 4). Lesions were counted and assessed based on their largest dimension. Scabs were considered a single lesion if forming a continuous line. A scratch exceeding 2 cm was classified as one lesion; two parallel scratches with a maximum separation of 0.5 cm were also counted as one lesion. Small lesions (<2 cm) were recorded as one lesion. Bleeding wounds 2–5 cm in length, as well as healed wounds >5 cm, were classified as five lesions. Deep, open wounds >5 cm were also recorded as five lesions.

Approximately 15 min after each PIT, once the animals had been moved into separate holding pens, a follow-up health assessment was conducted using the same protocol to quantify new lesions or potential lameness that may have developed during the PIT. All assessments were conducted by a single trained research assistant to ensure consistency.

2.5 Data formatting and statistical analysis

2.5.1 Aggregation of behavior variables and lesions prior to statistical analyses

To improve interpretability and analytical robustness, individual behavioral variables and lesion variables were conceptually

TABLE 2 Ethogram of observed behaviors and whether these were observed as a performed or a response behavior, and their corresponding behavioral category used in the analyses.

Behavior categories	Variable name	Definition	Performing behaviors observed	Response behaviors observed
Affiliative	Nosing	Snout is touching or is within sniffing distance of other pig.	Yes	Yes
Affiliative	Nibbling	The pig is touching with its nose and pushes, the pig can also have its jaw slightly open and use her teeth.	Yes	Yes
Damaging	Biting	The pig bites the other pig with its teeth in contact with the other pig's skin.	Yes	Yes
Damaging	Head knock	A rapid thrust upwards or sideways with the head or snout	Yes	Yes
Pressing	Parallel pressing	The pigs stand side by side (facing the same direction) and push hard with their shoulders against each other, throwing the head against the neck or head of the other.	Yes	Yes
Pressing	Inverse parallel pressing	The pigs stand front to front (facing opposite directions) and then push their shoulders hard against each other, throwing the head against the neck and flanks of the other.	Yes	Yes
Pressing	Press	The receiving pig presses her body (or face) against the performing pig	No	Yes
Warning	Threat	The pig stares and/or turns her head towards the other pig and stays, or she walks towards her, the other pig reacts.	Yes	No
Warning	Chewing	The pig performs chewing without anything in her mouth, one session is continuous chewing and a new one begins when the chewing has stopped with three second in-between until next chewing session.	Yes	No
Other	Levering	The pig puts its snout under the body of the other pig and lifts her up in the air, you can see that the body is pushed upwards but all legs can still be in the ground.	Yes	Yes
Other	Mouth open	The pig's mouth is open, but it is not biting or nibbling the other sow.	Yes	Yes
Other	Shaking	The sow rapidly shakes her body from side to side	Yes	No
Other	Climbing/riding	At least one hoof/leg on the top of another pig/mounting the other pig.	Yes	Yes
Retreat	Retreat	The sow moves away from the other sow, can be accompanied with a push to get by the other pig. Can also be that the pig moves the target body part away, for example turns her neck backwards or to the side to escape an attack to this area.	No	Yes
Threat	Threat	The pig stares and/or turns her head towards the other pig and stays, or she walks towards her, the other pig reacts.	No	Yes
No change	No change	The receiving pig does not react to the interaction of the other sow, standing still or continues what she was doing before the interaction.	No	Yes

aggregated into broader categories, taking into account both theoretical and practical considerations. Behavioral categories were based on ethological descriptions and interpretations of the presumed function of the behavior, whereas lesion categories were based on the presumed underlying cause of lesions on different parts of the body.

2.5.1.1 Social behaviors performed by the FPSs and older sows

Initiation of social interactions was grouped separately according to whether the initiating behavior was performed by the FPS or the older sow. The behaviors Nosing and Nibbling were aggregated into a category called Affiliative behaviors; Biting and Head knocks were aggregated as Damaging behaviors; Chewing and Threat were aggregated as Warning behaviors; Inverse parallel pressing and Parallel pressing were aggregated as Pressing; and Mouth open, Climbing/riding, Levering, and Shaking were grouped as Other behaviors (Table 2).

Because the focus of the study was on the FPSs' responses, only the response behaviors of the FPS, not the older sow, were analyzed. Behaviors performed by the FPS as a response to the older sow's behavior were grouped as follows: Affiliative behaviors and Damaging

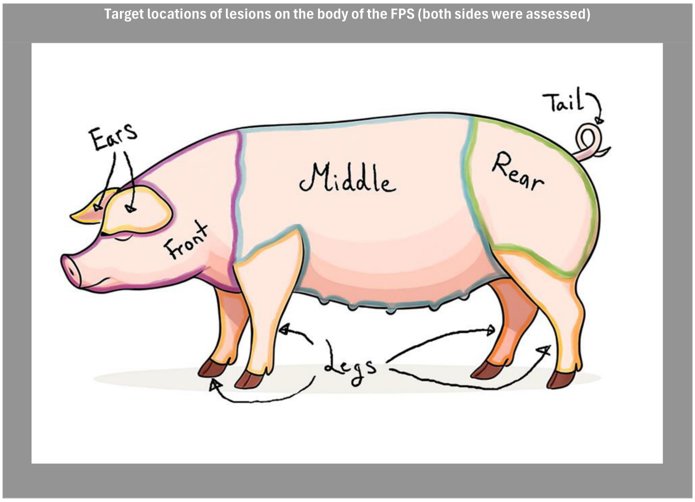


FIGURE 4
Illustration of the target locations assessed for skin lesions. Both left and right body sides were evaluated to account for potential asymmetries in lesion distribution. In the analysis, ears and front were grouped into a Front body region, and hindquarters and tail were grouped into a Rear body region.

behaviors as described above; Inverse parallel pressing, Parallel pressing, and *Press* were aggregated as Pressing; and Mouth open, Climbing/riding, and Levering were aggregated as Other behaviors. Response behaviors such as Retreat, Threat, and No change in behavior were not grouped, as these represent distinct response strategies with different functional meanings and were analyzed separately.

To study social interactions in more detail, we subsequently investigated the associations between the older sow's behavior toward the FPS (aggregated as described previously) and the FPS's response to this behavior (aggregated as described above).

2.5.1.2 Lesions on the FPS

Changes in lesion scores for the FPSs as a result of the PIT (lesion score after minus lesion score before the PIT) were aggregated into categories prior to statistical analysis based on the underlying cause of receiving lesions on different parts of the body (e.g., Welfare Quality, 2009, Turner et al., 2006). Lesions counted on the ears and front were categorized as Front; lesions on the hindquarters and tail were categorized as Rear. Lesions on the middle body region and legs were not aggregated into new categories, as they did not conceptually align with predefined lesion-location categories used in previous studies (e.g., Turner et al., 2006, Tönepöhl et al., 2013). In addition, the total number of lesions gained on the entire body during the PIT was analyzed.

2.5.1.3 Associations between behavior and lesions

To analyze associations between behavior and lesion outcomes, the same behavioral categories and lesion categories described above were applied. This ensured consistency across analyses and enabled meaningful comparisons with other results in this study.

2.5.2 Statistical analyses

Data from BORIS were exported and formatted in Microsoft® Excel® (Microsoft 365 MSO, Version 2502 Build 16.0.18526.20168) for statistical analyses. The PIT dataset included social-behavior recordings (a total of 8,225 behaviors registered during social interactions, including both initiating and response behaviors) and lesions from 79 PITs (one FPS per PIT).

All statistical analyses were conducted in R (version 4.3.1) (R Core Team, 2024). Generalized linear mixed models (GLMMs) were fitted using the glmmTMB package (Brooks et al., 2017). Model selection was based on a backward stepwise procedure starting from full models that included all biologically relevant fixed effects and interactions. At each step, interactions were removed, and models were compared using Akaike Information Criterion (AIC) values and model weights via the MuMIn package (Bartoń, 2025). Models excluding interaction terms fitted better and were therefore used as the final models.

Random effects (e.g., Pen, Old_batch, the batch in which the FPS was born) were also tested in preliminary models. For clarity and interpretability, the final models were GLMs without random effects. In most cases, models were fitted using a negative binomial distribution (family = nbinom2) due to overdispersion in the count data (variance > mean). Zero-inflated models were considered and used only when clearly superior based on AIC (e.g., for lesions on the middle part of the body). Model assumptions were evaluated based on best fit, assessed by AIC, residual diagnostics, and distributional properties (e.g., variance > mean).

2.5.2.1 Statistical models

Latency to first contact (seconds to first physical contact) was analyzed as a continuous outcome with Model 1. Based on the right-skewed distribution and lack of zero-inflation, a gamma model with a log link was used. To explore whether the FPS or the older sow initiated the first contact, *who approached first* was analyzed with Model 1 using binary logistic regression (1 = FPS initiated, 0 = sow initiated).

To examine how the frequency of *initiating and response behaviors and the lesions gained)* during the PIT *(points 1–4 below)* were influenced by genetic line, early social mixing environment, late social mixing environment, and season, models were fitted for each variable using glmmTMB with a negative binomial distribution. The variables analyzed were:

1. *performed by the FPS:* outcome variable *Y* = count of each specific initiating behavior summarized per FPS.
2. *performed by the older sow* toward the FPS: outcome variable *Y* = count of each specific initiating behavior by the older sow summarized per FPS.
3. *FPS response behaviors to interactions initiated by the opponent older sow*: Outcome variable *Y* = counts of each specific response behavior summarized per FPS).
4. *Lesion outcomes* (e.g., total lesions received during the PIT, lesions in specific body regions): Outcome variable *Y* = counts of each specific lesion summarized per FPS.

The final model fitted for variables 1–4 is Model 1.

Model 1: Y ~ Genetic line + Early social mixing environment + Late social mixing environment + Quarter + e.

To investigate whether the *FPS responded differently depending on the behavior performed by the older sow*, GLMMs were analyzed separately for each behavior category using Model 2, fitted with glmmTMB using a negative binomial distribution (family = nbinom2). The response variable (n) represented the number of times a specific behavior was observed for an FPS in response to each initiating behavior performed by the older sow, derived by aggregating the dataset using dplyr::summarize() in R.

Only sow-behavior categories with sufficient variability and complete data across grouping variables were retained. Models were successfully estimated for Damaging behaviors, Affiliative behaviors, and Warning behaviors. Categories with sparse data, such as Press and Other performed by the older sows, as well as Damaging behaviors and Other demonstrated by the FPSs, were excluded due to insufficient frequencies (fewer than 30 observations in total), to ensure analytical robustness and avoid convergence issues.

For Model 2, *Y* was the count of each response behavior per FPS relative to each older sow behavior performed during the PIT. The interaction between older sow behavior and genetic line, early social mixing environment, and late social mixing environment was assessed to determine whether response patterns varied by genetic line or social mixing conditions. Analyses were conducted separately for each sow-behavior category to capture behavior-specific dynamics. Only older sow behaviors with sufficient data across all combinations were included. Specifically, robust models were fitted for Damaging behaviors, Affiliative behaviors, and Warning behaviors, which were the only categories with enough observations. Behaviors with sparse data (e.g., Press and Other) were excluded due to low frequency and model-convergence issues.

Associations between behavior and lesions were analyzed using regression analyses with generalized linear models (GLMs) with a negative binomial distribution (family = nbinom2). These models were fitted for each behavioral category variable (performed, response, or directed at the FPS) and each lesion outcome (Total, Front, Rear, Middle, and Legs) using Model 3, where Y was the lesion count per FPS (either total change or region-specific counts).

*Model 2: Y ~ Older sow behavior *Genetic line + Older sow behavior * Treatment_1 + Older sow behavior * Treatment_2 + e.*

For Model 2, model performance and interaction significance were evaluated using Type III Wald chi-square tests (drop1, test = "Chisq"). Estimated marginal means (LSMeans ± SE) and Tukey-adjusted pairwise contrasts ($\alpha = 0.05$) were calculated using the emmeans package. Significant differences between FPS response behaviors were visualized using grouped bar plots with error bars and annotated horizontal brackets indicating significant pairwise comparisons.

*Model 3: Y ~ Behavior * Genetic line + Behavior * Treatment 1 + Behavior * Treatment 2 + e.*

For Model 3, Behavior refers to the predictor variable, representing either behaviors performed by the FPS, behaviors directed against the FPS by the older sow, or FPS response behaviors following social interactions. The specific predictor variables were placed as interactions with Genetic line, Early social mixing environment, and Late social mixing environment. In Model 3, interaction terms were explicitly included to detect potential moderation effects of social background and genetic line on the behavior–lesion relationship.

The variable Quarter was added as a fixed effect to adjust for seasonal variation but was not interpreted. The models for associations between behavior and lesions were fitted using glmmTMB, and fixed-effect estimates (β), corresponding risk ratios [$RR = \exp(\beta)$], and p-values were extracted using the broom.mixed package. Results were automatically structured by behavior type and exported to Excel using writexl, with separate sheets for all effects, significant effects, all interactions, and significant interactions. This approach enabled comprehensive detection of context-specific behavioral risk patterns for skin lesions.

For Models 1, 2, and 3, the predictor variables were defined as follows:

: *Genetic line* represents the FPS breed (Swedish Yorkshire [SY] or Dutch Yorkshire [DY]); *Early social mixing environment* indicates whether the FPS had access to early mixing with non-littermates (access pen [AP] *vs.* closed pen [CP]); *Late social mixing environment* describes whether FPSs were housed in mixed groups (MG) or intact groups (IG) after 10 weeks of age.

In Models 1 and 3, *Quarter* (Q1–Q4) was included as a fixed effect to denote the time of year the test was conducted and to control for potential seasonal variations; however, its effects were not interpreted. Interaction terms were tested in all models but were excluded from the final Model 1 due to multicollinearity or lack of improvement in model fit.

Estimated marginal means (EMMs) and *post hoc* comparisons were calculated using the emmeans package (Lenth et al., 2025) for models with significant fixed effects. Pairwise contrasts and confidence intervals were used to explore the direction and strength of effects. Statistical significance was set at p < 0.05.

3 Results

The core results are presented below. Descriptive statistics and tables with p-values are provided as Supplementary Material. Results are presented as LS-means ± SE unless otherwise stated.

3.1 Latency to first contact and who approached first

Latency for the two sows to approach each other in the PIT was on average 10.6 s (SD = 11.47 s). There were no significant effects of genetic line or early or late social mixing environment on the latency for the two sows to approach each other in the PIT. In total, FPSs initiated contact in 76% of PITs. There were no significant effects of genetic line or social mixing environments on whether the FPS or the older sow approached first.

3.2 Behaviors initiating social interactions in the PIT

3.2.1 Initiating behaviors by the FPS towards the older sow

FPSs from the AP treatment demonstrated significantly more affiliative behaviors than FPSs from the CP treatment (19.1 ± 2.62 and 12.7 ± 1.68, respectively; F = 4.56, df = inf, p = 0.033). FPSs of the SY line performed significantly more damaging behaviors than FPSs of the DY line (23.39 ± 6.02 and 6.98 ± 1.80, respectively; F = 10.40, df = inf, p = 0.001) and also more warning behaviors (15.88 ± 1.77 and 8.99 ± 0.97, respectively; F = 12.84, df = inf, p < 0.001). The late social mixing environment had no significant effects on FPS-initiated behaviors.

3.2.2 Initiating behaviors by the older sow towards the FPS

Damaging behaviors were significantly more often directed toward SY compared to DY FPSs (34.6 ± 5.07 and 20.8 ± 2.91 times per FPS, respectively; F = 5.86, df = inf, p = 0.016). Pressing was also significantly more frequently performed against SY than DY FPSs (1.87 ± 0.33 and 1.03 ± 0.20 times per FPS, respectively; F = 5.00, df = inf, p = 0.025). Neither early nor late social mixing environment had significant effects on older-sow-initiated behaviors.

3.3 Response behaviors during social interactions in the PIT

3.3.1 General FPS behavior responses

Damaging behaviors performed as FPS responses to older-sow-initiated interactions occurred significantly more often among SY FPSs compared to DY FPSs (1.54 ± 0.51 and 0.26 ± 0.12 times per FPS, respectively; F = 9.45, df = inf, p = 0.002). Pressing was also a more common response among SY compared to DY FPSs (27.00 ± 5.20 and 14.00 ± 2.59 times per FPS, respectively; F = 5.53, df = inf, p = 0.019).

FPSs from the AP early social mixing environment showed *no* change in behavior significantly more often than FPSs from the CP treatment (4.29 ± 0.77 and 2.07 ± 0.51 times per FPS, respectively; F = 4.29, df = inf, p = 0.038). The late social mixing environment had no significant effects on FPS response behaviors.

3.3.2 FPSs' response behaviors classified according to older sow behaviors

Frequencies of response behaviors by FPSs, according to the type of behavior the older sow showed when initiating the social interaction, is presented in Table 3. Differences in FPS responses

TABLE 3 Frequencies of response behaviors displayed by the first parity sows (FPS) in relation to the type of behavior initiated by the older sow during a social interaction.

		Response behavior by FPS						
		Damaging behavior	Affiliative behavior	No change	Press	Threat	Retreat	Other
Behavior of old sows	Damaging behavior	24	7	16	70	14	72	3
	Affiliative behavior	1	55	50	22	27	71	0
	Warning behavior	0	1	1	0	41	76	0
	Press	0	1	0	50	0	2	0
	Other	1	0	3	16	1	5	0

Rows represent the type of behavior performed by the older sow at the onset of the interaction, and columns indicate the FPSs response behavior to that specific behavior. Frequencies denote the total number of observed interactions per behavior combination.

according to the older sow's initiating behavior are presented in Figure 5. No significant interactions were found between the older sow's initiating behavior and the genetic line of the FPS (p < 0.056), their early social mixing environment (p < 0.31) or late social mixing environment (p < 0.28).

3.4 Occurrence of lesions on FPS

The increase in total lesions from before to after the PIT was significantly higher for SY FPSs than for DY FPSs (4.29 ± 0.98 and 2.07 ± 0.51, respectively; F = 8.45*, df = inf, p = 0.005). SY FPSs also had significantly more lesions on the front body region (6.42 ± 1.38 and 3.33 ± 0.69 per FPS, respectively; F = 4.52, df = inf, p = 0.034) and the rear body region (3.11 ± 1.17 and 0.98 ± 0.37 per FPS, respectively; F = 4.30, df = inf, p = 0.038). A similar pattern was observed for lesions on the legs, where SY FPSs had significantly more lesions than DY FPSs (1.06 ± 0.43 and 0.27 ± 0.12 per FPS, respectively; F = 5.44, df = inf, p = 0.020). There were no significant effects of early or late social mixing environment.

3.5 Associations between behavior and lesion count on the FPSs

Increased frequencies of damaging and warning behaviors performed by the FPSs were associated with elevated lesion counts on the front of the body (β = 0.03, RR = 1.03, p = 0.012; and β = 0.06, RR = 1.06, p = 0.039, respectively). Affiliative behaviors performed by the older sows were associated with reduced total lesion counts on the FPSs (β = −0.08, RR = 0.92, p = 0.018).

Regarding FPS response behaviors to interactions initiated by the older sow, both retreat and threat were associated with a decreased number of lesions on the front of the body (retreat: β = -0.05, RR = 0.95, p=0.023; threat: β = -0.06, p=0.008) and in total (retreat: β = - 0.06, RR = 0.94, p=0.008; threat: β = -0.59, RR = 0.55, p=0.004). Increased amounts of affiliative behaviors performed by FPSs in response to interactions initiated by the older sow were associated with fewer lesions on the rear of the body (β = −1.71, RR = 0.18, p = 0.017). In contrast, increased damaging behavior by the FPS in response to an older sow's initiation was associated with increased lesion counts on the front of the body (β=0.31, RR = 1.03, p=0.046).

3.5.1 Interaction effects

Significant interactions were sparse, indicating similar behavior–lesion associations across genetic lines and social mixing environments. However, a consistent pattern was observed for pressing behaviors.

FPSs of the DY line that exhibited higher frequencies of pressing were more likely to have increased lesion scores on the rear of the body and in total (Rear: β = 1.14, RR = 3.14, p = 0.010; Total: β = 0.40, RR = 1.49, p = 0.048), which was not the case for FPSs of the SY line.

Regarding early social mixing environments, FPSs from the CP treatment (i.e., without early social mixing) that performed pressing

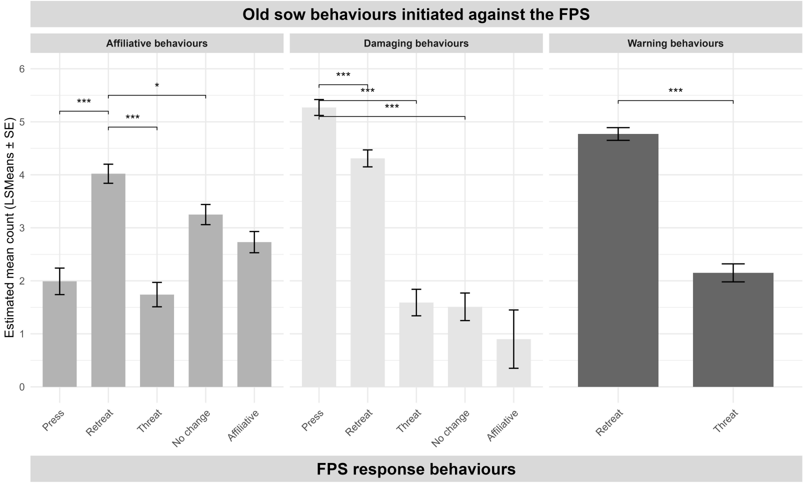


FIGURE 5
Response behaviors of first parity sows (FPS) following three types of behaviors exhibited by the older sow during the paired interaction test (PIT). Bars represent estimated mean counts (LSMeans ± SE) of each response behavior, separated by the older sow's behavior. Only behaviors with sufficient data to estimate model parameters are shown. Horizontal brackets indicate pairwise comparisons between FPS response behaviors within each sow behavior category, based on model estimates. Significance levels are denoted as follows: p < 0.05 (*), and p < 0.001 (***).

behaviors had more lesions on both the rear of the body and in total (Rear: β = 1.06, RR = 2.90, p = 0.016; Total: β = 0.41, RR = 1.51, p=0.043). This pattern was not observed among FPSs from the AP treatment. A similar effect occurred when older sows performed pressing toward FPSs from the CP treatment, resulting in more lesions (β = 0.36, RR = 1.43, p = 0.031) compared to pressing toward FPSs from the AP treatment.

Performance of affiliative behaviors was linked to fewer front-body lesions for FPSs of the DY line (β = −0.06, RR = 0.95, p = 0.034). However, affiliative behaviors performed by older sows toward DY FPSs were associated with increased lesion counts on the front (β = 0.06, RR = 1.07, p = 0.026) and in total (β = 0.06, RR = 1.07, p = 0.043). FPSs of the DY line that responded with affiliative behaviors also received more lesions on the rear of the body (β = 1.14, RR = 3.13, p = 0.049) than FPSs of the SY line.

Retreat performed by FPSs as a response to older sow behavior was strongly associated with increased total lesions among DY FPSs (β = 0.05, RR = 1.05, p = 0.011), but not among SY FPSs. Likewise, threat behaviors performed by DY as a response to a social interaction by the older sow led to increased lesion counts on both the front (β = 0.42, RR = 1.52, p = 0.012) and in total (β = 0.37, RR = 1.44, p = 0.013), a pattern not observed in SY FPSs.

Furthermore, retreat as a response behavior by FPSs raised in the MG late social mixing environment was associated with increased lesions both on the front (β = 0.05, RR = 1.05, p = 0.038) and in total (β = 0.05, RR = 1.05, p = 0.022). A similar pattern was observed for MG FPSs responding with threat, as they received more lesions on the front (β = 0.34, RR = 1.41, p = 0.044).

FPSs from the MG treatment that performed damaging behaviors received fewer lesions on the front part of the body (β = −0.02, RR = 0.98, p = 0.039) compared to FPSs from the IG treatment, which remained intact and did not experience late social mixing.

4 Discussion

This study aimed to investigate how genetic lines and social mixing environments during early and late gilt rearing influence social behavior, social responsiveness, and the number of skin lesions in first-parity sows (FPSs) during pairwise interaction tests with an older sow (PIT). The PIT was carried out after the FPS's litter had been weaned, which is when they would typically be moved to group housing.

Our findings revealed effects of genetic line across several aspects of the social interactions analyzed in this study. In contrast to our prediction, FPSs of the SY line performed higher frequencies of damaging and warning behaviors toward older sows, received more damaging and pressing behaviors, responded more frequently with damaging and pressing behaviors to older-sow-initiated interactions, and accumulated more skin lesions.

In line with our prediction, there were indications that early social mixing experiences affected the number of affiliative behaviors performed toward older sows. FPSs from the access pen (AP) treatment demonstrated significantly more affiliative behaviors when initiating social interactions. They were also more likely to be neutral (i.e., show no behavioral change) following a social interaction initiated by the older sow.

On the other hand, FPSs with late social mixing experience (the MG treatment) showed no consistent main effects on behavior or lesion counts across the full dataset, although behavior-specific effects emerged. FPSs reared in the MG environment received fewer lesions on the front part of the body when performing damaging behaviors, whereas MG FPSs responding with threat or retreat were more likely to sustain front and total lesions. These findings suggest that late social mixing during rearing may shape how individuals react to aversive social interactions, rather than directly modifying overall levels of aggression or affiliative behaviors.

4.1 Genetic line influences social behavior and risk for skin lesion

A consistent pattern emerged across outcome measures, indicating that FPSs of the SY genetic line were more socially engaged than FPSs of the DY line. SY FPSs displayed higher frequencies of both damaging and warning behaviors directed toward the older sow in the PIT and were also more likely to receive such behaviors. This reciprocal pattern suggests a generally higher level of social involvement and/or a more proactive communication style, which is consistent with lower thresholds for contest engagement in more proactive profiles (demonstrated predominantly among younger pigs [Bolhuis et al., 2005)]; however, evidence among adult breeding females is context-dependent (Geverink et al., 2002; Janczak et al., 2003).

SY FPSs also accumulated significantly more lesions following the PIT, notably on the front of the body, the rear, and the legs. Lesions on the front are typically associated with reciprocal or mutual aggression, while lesions on the rear often reflect retreating or defensive behaviors (Turner et al., 2006; Turner et al., 2008). This lesion distribution in SY FPSs supports the interpretation that they were more deeply engaged in agonistic behaviors, both initiating and responding with such behaviors.

Affiliative behaviors had context-dependent associations with lesion outcomes, particularly among FPSs of the DY genetic line. Affiliative behaviors are often used as indicators of social bonds among pigs and sow herds (Durrell et al., 2003; Camerlink et al., 2022). Although post-conflict affiliation has been shown to buffer anxiety in pigs (Norscia et al., 2021), our findings suggest a more nuanced role in FPS lesion outcomes. Affiliative behaviors performed by DY FPSs were linked to fewer lesions, potentially indicating a conflict-dampening effect when initiated by the FPSs themselves. However, affiliative behaviors directed toward DY FPSs by older sows, or used by DY FPSs in response to social interactions, were associated with increased lesions in several body regions. These patterns indicate that affiliative behaviors, especially in tense or unresolved social contexts, may not always reflect harmonious interactions.

While post-conflict affiliation may help de-escalate interactions (Norscia et al., 2021) and buffer the effects of agonistic encounters

(Rault, 2012), our findings suggest that affiliation does not uniformly suppress aggression. Similar co-occurrence of affiliative and contest behaviors has been observed during socially unstable periods in finisher pigs (O'Malley et al., 2022). Thus, affiliative interactions should be interpreted with caution, especially in early-stage encounters, as their meaning and welfare implications may depend on both social experience and genetic background.

Although aggression is often viewed negatively from a welfare perspective, given links between repeated injury, stress, and compromised health (Verdon et al., 2015; Maes et al., 2016), the social intensity observed among SY FPSs in the present study may facilitate the rapid formation of dominance hierarchies and more stable group dynamics in the long term (Arey and Edwards, 1998; Verdon et al., 2015). It is important to note that no FPS had to be removed from the group due to injuries sustained during the PIT, indicating that although lesion counts were higher in SY than DY FPSs, the overall severity remained low.

In line with our initial expectations regarding differences in social reactivity, these findings suggest that SY FPSs may express a more socially assertive interaction style in this context. Such assertiveness may hasten rank clarification when competition is constrained but could also elevate short-term injury risk (as reflected in front- and rear-body lesion patterns). In contrast, DY FPSs may follow a more conservative strategy that could reduce immediate risk but potentially prolong uncertainty under contested resources. If so, selection decisions may need to be environment-dependent, considering social-behavior indicators alongside production traits and management strategies that limit contest costs.

4.2 Early social mixing shows associations with affiliative behaviors and responsiveness

The results suggest that early social mixing experiences shaped the social interaction style of the FPSs, particularly within affiliative contexts. FPSs from the AP group displayed more affiliative behaviors than those from the CP group, which aligns with earlier findings that early-life socialization fosters prosocial tendencies and improves social competence (Kutzer et al., 2009; Salazar et al., 2018). This indicates that exposure to unfamiliar conspecifics during early development enhances pigs' capacity for social engagement.

Notably, FPSs from the AP group were also more likely to maintain their behavior—i.e., show "*no* change"—when approached by an older sow. Such neutral responses may reflect social tolerance or a less proactive coping style (Rault, 2017). Alternatively, "*no* change" may indicate habituation due to early social exposure, leading to reduced reactivity to unfamiliar sows, as seen in studies with younger pigs (D'Eath, 2005; Morgan et al., 2014).

Despite these behavioral differences, early social mixing did not influence the likelihood of receiving damaging behaviors, nor did it affect total lesion outcomes. This is consistent with evidence that early socialization can shape social style without necessarily reducing aggression or injuries under competitive challenge (van Nieuwamerongen et al., 2017; Camerlink et al., 2018). Thus, affiliative tendencies may coexist with high social engagement without necessarily lowering the risk of aggressive encounters once competition arises.

Taken together, these findings are consistent with earlier research, primarily from piglets and grow, finisher pigs, which shows that pre-weaning socialization influences later interaction style and can increase affiliative behaviors and social skills/tolerance (Van Putten and Buré, 1997; D'Eath, 2005; Morgan et al., 2014; Camerlink et al., 2018). The results of this study may extend this pattern to FPSs post-weaning.

Future research should assess whether early socialization improves long-term social behavior and group dynamics among sows, since the current dyadic testing setup did not allow evaluation of group-level processes such as hierarchy formation or social stability.

4.3 Context-dependent effects of late social mixing environment

The late gilt-rearing social mixing experience showed no consistent main effects on performed behaviors, received behaviors, response types, lesion outcomes, or latency to contact. This was somewhat unexpected, as prior studies have shown that post-weaning regrouping and group composition can alter aggression (Colson et al., 2006) and elevate physiological stress (Otten et al., 2002).

One explanation may be that although the FPS and older sow were unfamiliar to each other, mixing only two individuals created a relatively small social disturbance, with limited competition. This may have kept post-mixing aggression brief and less intense, particularly when structural features allow avoidance (hay bale) and reduce direct confrontation (e.g., sufficient floor area for withdrawal, bedding, and visual barriers) (Arey and Edwards, 1998; Greenwood et al., 2014). Group size, timing, and the predictability of mixing events are key moderators of regrouping outcomes.

In the present study, FPSs in the MG treatment had been co-housed for an extended period before the PIT, which may have diminished short-term effects.

No effects of MG were found on overall behavioral frequencies or lesion scores across the full dataset; however, effects emerged when specific behaviors were examined. FPSs from the MG group that performed damaging behaviors received fewer lesions on the front of the body. Because front lesions are associated with reciprocal fighting (Turner et al., 2009; Turner et al., 2008), this may indicate that MG FPSs were involved in fewer reciprocal damaging interactions or used more effective engagement strategies in agonistic encounters.

In contrast, MG FPSs that responded with retreat or threat accumulated more lesions on the front and in total, a pattern consistent with greater exposure to aggression in less favorable body positions (O'Connell et al., 2003). This suggests that late social mixing may influence how sows cope with social challenges depending on the behavioral strategy employed.

It is also possible that the PIT, an interaction with a single unfamiliar individual in an unfamiliar setting, highlighted the pigs' early-life experiences and inherent behavioral traits more than their recent home-pen social environment. Late social mixing did not show consistent overall effects in the PIT setting. However, this does not rule out the possibility that such effects could emerge in a group-housing system with a larger group or under different management conditions.

4.4 FPSs' behavioral responses to older sows' behavior

The behavioral responses of FPSs varied depending on the type of behavior displayed by the older sow initiating the social interactions and were not affected by genetic line or social mixing experience when including the older sow's behavior. *Retreat* was the most frequent response across all behavior categories in the raw data, particularly following *affiliative*, *damaging*, and *warning behaviors*, suggesting a generally avoidant coping style in these short-term PIT encounters. However, the modeled comparisons revealed a more nuanced response pattern.

When older sows displayed *affiliative behaviors*, FPSs were significantly more likely to *retreat* than to respond with *affiliative*, *neutral*, or *threat behaviors*. This suggests that affiliative signals were not consistently interpreted or reciprocated as prosocial opportunities (Camerlink et al., 2014; O'Malley et al., 2022), possibly due to uncertainty in a novel context or a lack of established social familiarity (Arey and Edwards, 1998; Kranz et al., 2022). Rather than fostering social engagement, these cues appeared to trigger social retreat in this PIT.

In contrast, when exposed to *damaging behaviors*, FPSs mostly responded with either *pressing* or *retreating*, significantly more frequently than affiliative or passive responses. This dual strategy likely reflects context-dependent conflict coping, balancing active resistance with tactical retreat (Bolhuis et al., 2005). It may also reflect the intensity of the incoming threat, where *retreat* is the default but some individuals still engage physically in return (Arey and Edwards, 1998).

Warning behaviors from the older sows, i.e., a lower-intensity signal often interpreted as a threat of escalation (Camerlink et al., 2018), also predominantly elicited retreat. The preference for retreating over responding with a threat or engagement supports the idea that FPSs prioritized de-escalation/avoidance, which has been observed in earlier studies of dry sows (Jensen, 1982), in response to ambiguous or mild threat signals. This behavioral inhibition may reflect adaptive conflict avoidance but could also indicate heightened social caution in novel interactions.

Together, these results suggest that FPS responses were not indiscriminate but flexibly adjusted to the presented social information. The decision to retreat, even in response to *affiliative behaviors*, may reflect a generally cautious social strategy (Arey and Edwards, 1998), shaped by the unfamiliar testing context and the apparent dominance of the older sow. Retreat may function as an adaptive short-term response to perceived social threat, preventing escalation during potentially risky encounters.

This interpretation is supported by previous findings identifying "Avoider" phenotypes in group-housed sows, characterized by low engagement in aggressive interactions and fewer lesions shortly after mixing (Brajon et al., 2021). However, reliance on such avoidant strategies over time has been associated with increased lesion scores later in the group-housing period (Brajon et al., 2021), possibly due to impaired access to resources, reduced social support, or heightened chronic stress vulnerability. Hence, while *retreat* may offer short-term protection, it could also limit opportunities for affiliative bonding and social learning.

Overall, these findings highlight the importance of interpreting response behaviors in relation to the initiating social context and recognizing their potential long-term welfare consequences. In this study, while there were effects of early-life social experience, the results suggest that situational appraisal and social novelty remained important under the controlled conditions of the PIT.

4.5 Social initiative and latency to interaction

Most FPSs initiated the first contact with the older sow, regardless of treatment or genetic background, and there were no significant differences in latency to first contact. This suggests that the general motivation to engage socially was high and not clearly differentiated by social mixing environments or genetic lines.

4.6 Methodological considerations and study design reflections

This study employed a category strategy whereby semantically and functionally related behaviors (e.g., *nibbling, head knock, parallel pressing*) were aggregated into broader categories such as *affiliative, damaging*, and *warning behaviors*. Lesions were likewise grouped into anatomically meaningful regions (e.g., front, rear, legs) based on their functional relevance and previous links to social aggression (Turner et al., 2006; Turner et al., 2008). The categories were evidence-based, but we cannot exclude the possibility that another aggregation strategy might have produced different results. Nevertheless, this approach allowed for more meaningful interpretation of social strategies, as isolated actions, such as a single nibble or a lesion on the ear, are difficult to assess without contextual cues. This strategy supported robust and interpretable analyses of complex social behavior and, in particular, a more meaningful interpretation of social strategies.

The standardized PIT setup provided a controlled environment to isolate social response tendencies, but it lacks the dynamic complexity of commercial sow group housing. As a result, generalizability to larger, mixed-age groups or more competitive resource settings is limited. Certain behaviors observed here, such as high retreat rates, may reflect context-specific strategies that differ in commercial environments where more conspecifics are present. On the other hand, a key advantage of the PIT setup is the potential to integrate more detailed information, e.g., physiological data and vocalizations, in future studies.

Across all models, interaction terms were sparse: the links between specific behaviors and lesion patterns were largely consistent across genetic lines and rearing treatments. Within this controlled 60-minute PIT, injury risk appeared to reflect immediate, encounter-level strategies more than background factors. Methodologically, this supports the value of combined behavior–lesion indices as robust indicators of social risk in dyadic tests. However, we note that subtle moderation, which could have continued for several days and weeks, would have gone undetected. Thus, future work should interactions over extended time frames.

In summary, this study's controlled test design, combined with behavioral and lesion categories, enabled clear detection of group-level patterns relevant to welfare. However, interactions were tested only in pairs of sows over a short period, whereas under commercial conditions pigs are housed in larger groups for much longer. More research linking behavior and lesion outcomes in group settings is needed to identify which FPSs are best suited for group housing systems and to understand how social strategies affect welfare over time.

4.7 Implications for welfare and future directions

To summarize, the findings of the present study suggest that genetic background and early-life social experiences influence how young sows engage in social interactions and their associated risk of physical harm. The observed differences between genetic lines in behavior and lesion accumulation during the PIT were consistent across several measures, though these patterns need to be confirmed in larger groups.

Likewise, early social mixing experience appeared to promote affiliative tendencies and certain passive response strategies but did not clearly reduce the risk of receiving injuries within the short time frame of the test.

From an animal welfare perspective, the combined behavioral and lesion-based outcomes offered a useful framework for assessing social dynamics and identifying risks of negative experiences. Such indicators may serve as valuable tools for developing on-farm methods to monitor sow welfare in group-housed systems.

Future studies should examine how these indicators manifest under commercial conditions with larger groups and over longer periods, and whether combinations of early-life interventions and genotype-informed group structuring, i.e., grouping sows based on behavioral tendencies associated with genetic line, can help mitigate social conflict and reduce injury risk.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by the National Ethics Committee for Animal Experiments in Uppsala (Registration number: 5.8.18-16279/2017). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

LMBH: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. LK: Conceptualization, Funding acquisition, Methodology, Writing – review & editing, Supervision. AW: Conceptualization, Formal analysis, Funding acquisition, Methodology, Writing – review & editing, Project administration, Supervision.

Funding

The author(s) declared that financial support was received for the research and/or publication of this article. This research was funded by FORMAS, reference number: 2016-01787.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Generative AI statement

The author(s) declare that Generative AI was used in the creation of this manuscript. ChatGPT (OpenAI; model GPT-5, accessed Sep 2025) and Grammarly (Grammarly Inc.; v.1.2.196.1758) were used solely for language editing and formatting. All scientific content, analyses, and conclusions were developed and verified by the authors, who take full responsibility for the manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fanim.2025.1711609/full#supplementary-material

References

Albernaz-Gonçalves, R., Olmos, G., and Hötzel, M. (2021). My pigs are ok, why change? – animal welfare accounts of pig farmers. *Animal* 15, 100154. doi: 10.1016/j.animal.2020.100154

Arey, D. S., and Edwards, S. A. (1998). Factors influencing aggression between sows after mixing and the consequences for welfare and production. *Livestock Product. Science.* 56, 61–70. doi: 10.1016/S0301-6226(98)00144-4

(1988). *Djurskyddsförordning (1988:539).* Available online at: https://www.riksdagen.se/sv/dokument-och-lagar/dokument/svensk-forfattningssamling/djurskyddsforordning-1988539_sfs-1988-539/ (Accessed March 19, 2025).

(2019). *Djurskyddsförordning (2019:66).* Available online at: https://www.riksdagen.se/sv/dokument-och-lagar/dokument/svensk-forfattningssamling/djurskyddsforordning-201966_sfs-2019-66/ (Accessed March 19, 2025).

Backeman Hannius, L. M., Keeling, L., de Oliveira, D., Anderson, C., and Wallenbeck, A. (2024). Friend or foe: effects of social experience and genetic line on responses of young gilts in a social challenge paired interaction test. *Animal* 18, 101349. doi: 10.1016/j.animal.2024.101349

Barnett, J. L., Hemsworth, P. H., Cronin, G., Jongman, E. C., and Hutson, G. D. (2001). A review of the welfare issues for sows and piglets in relation to housing. *Aust. J. Agric. Res.* 52, 1–28. doi: 10.1071/AR00057

Bartoń, K. (2025). *MuMIn: Multi-Model Inference*. Available online at: https://cran.r-project.org/web/packages/MuMIn/index.html (Accessed September 11, 2025).

Bolhuis, E., Schouten, J., Schrama, W. G. P., and Wiegant, V. M. (2005). Individual coping characteristics, aggressiveness and fighting strategies in pigs. *Anim. Behaviour.* 69, 1085–1091. doi: 10.1016/j.anbehav.2004.09.013

Boyle, L., Carroll, C., Mccutcheon, G., Clarke, S., McKeon, M., Lawler, P., et al. (2012). *Towards January 2013: Updates, implications and options for group housing pregnant sows* (Agriculture and Food Development Authority, Fermoy, Co. Cork, Ireland: Pig Development Department, TEGASC).

Brajon, S., Ahloy-Dallaire, J., Devillers, N., and Guay, F. (2021). Social status and previous experience in the group as predictors of welfare of sows housed in large semi-static groups. *PloS One* 16 (6), e0244704. doi: 10.1371/JOURNAL.PONE.0244704

Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A., et al. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 378–400. doi: 10.32614/RJ-2017-066

Camerlink, I., Farish, M., D'eath, R. B., Arnott, G., and Turner, S. P. (2018). Long term benefits on social behaviour after early life socialization of piglets. *Animals* 8, 192. doi: 10.3390/ani8110192

Camerlink, I., Scheck, K., Cadman, T., and Rault, J.-L. (2022). Lying in spatial proximity and active social behaviours capture different information when analysed at group level in indoor-housed pigs. *Appl. Anim. Behav. Science.* 246, 105540. doi: 10.1016/j.applanim.2021.105540

Camerlink, I., Turner, S. P., Farish, M., and Arnott, G. (2015). Aggressiveness as a component of fighting ability in pigs using a game-theoretical framework. *Anim. Behaviour.* 108, 183–191. doi: 10.1016/J.ANBEHAV.2015.07.032

Camerlink, I., Turner, S. P., Farish, M., and Arnott, G. (2019). Advantages of social skills for contest resolution. *R. Soc. Open Science.* 6, 1-8. doi: 10.1098/rsos.181456

Camerlink, I., Turner, S. P., Ursinus, W. W., Reimert, I., and Bolhuis, J. E. (2014). Aggression and affiliation during social conflict in pigs. *PloS One* 9, e113502. doi: 10.1371/journal.pone.0113502

Chapinal, N., Ruiz de la Torre, J. L., Cerisuelo, A., Gasa, J., Baucells, M. D., Coma, J., et al. (2010). Evaluation of welfare and productivity in pregnant sows kept in stalls or in 2 different group housing systems. *J. Veterinary Behavior.* 5, 82–93. doi: 10.1016/j.jveb.2009.09.046

Colson, V., Martin, E., Orgeur, P., and Prunier, A. (2012). Influence of housing and social changes on growth, behaviour and cortisol in piglets at weaning. *Physiol. Behavior.* 107, 59–64. doi: 10.1016/J.PHYSBEH.2012.06.001

Colson, V., Orgeur, P., Courboulay, V., Dantec, S., Foury, A., and Mormède, P. (2006). Grouping piglets by sex at weaning reduces aggressive behaviour. *Appl. Anim. Behav. Science.* 97, 152–171. doi: 10.1016/j.applanim.2005.07.006

Council of the European Union (2008). Council Directive 2008/120/EC laying down minimum standards for the protection of pigs. *Off. J. Eur. Union*, L47/5–L4713.

Coutellier, L., Arnould, C., Boissy, A., Orgeur, P., Prunier, A., Veissier, I., et al. (2007). Pig's responses to repeated social regrouping and relocation during the growing-finishing period. *Appl. Anim. Behav. Science.* 105, 102–114. doi: 10.1016/j.applanim.2006.05.007

D'Eath, R. B. (2004). Consistency of aggressive temperament in domestic pigs: The effects of social experience and social disruption. *Aggressive Behavior.* 30, 435–448. doi: 10.1002/AB.20077

D'Eath, R. B. (2005). Socialising piglets before weaning improves social hierarchy formation when pigs are mixed post-weaning. *Appl. Anim. Behav. Science.* 93, 199–211. doi: 10.1016/j.applanim.2004.11.019

D'Eath, R. B., and Pickup, H. E. (2002). Behaviour of young growing pigs in a resident-intruder test designed to measure aggressiveness. *Aggressive Behavior.* 28, 401–415. doi: 10.1002/AB.80010

D'Eath, R. B., and Turner, S. (2010). "The natural behaviour of the pig," in *The Welfare of Pigs*. Ed. J. Marchant-Forde (Springer Science, Brisbane, QLD, Australia), 13–45.

Dingemanse, N. J., and Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: Causes and consequences. *Anim. Behaviour.* 85, 1031–1039. doi: 10.1016/j.anbehav.2012.12.032

Durrell, J. L., Beattie, V. E., Sneddon, I. A., and Kilpatrick, D. (2003). Pre-mixing as a technique for facilitating subgroup formation and reducing sow aggression in large dynamic groups. *Appl. Anim. Behav. Science.* 84, 89–99. doi: 10.1016/j.applanim.2003.06.001

Engblom, L., Lundeheim, N., Dalin, A. M., and Andersson, K. (2007). Sow removal in Swedish commercial herds. *Livestock Science.* 106, 76–86. doi: 10.1016/J.LIVSCI.2006.07.002

European Commission (2023). Attitudes of Europeans towards animal welfare *(Special Eurobarometer 533)* (Brussels: Directorate-General for Communication). Available online at: https://europa.eu/eurobarometer/surveys/detail/2996 (Accessed October 22, 2025).

Friard, O., and Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evolution.* 7, 1325–1330. doi: 10.1111/2041-210X.12584

Geverink, N. A., Schouten, W. G. P., Gort, G., and Wiegant, V. M. (2002). Individual differences in aggression and physiology in peri-pubertal breeding gilts. *Appl. Anim. Behav. Science.* 77, 43–52. doi: 10.1016/S0168-1591(02)00024-2

Gonyou, H. W. (2005). Experiences with alternative methods of sow housing. *J. Am. Veterinary Med. Assoc.* 226, 1336–1340. doi: 10.2460/javma.2005.226.1324

Goumon, S., Illmann, G., Leszkowová, I., Dostalová, A., and Cantor, M. (2020). Dyadic affiliative preferences in a stable group of domestic pigs. *Appl. Anim. Behav. Science.* 230, 105045. doi: 10.1016/j.applanim.2020.105045

Greenwood, E. C., Plush, K. J., van Wettere, W. H. E. J., and Hughes, P. E. (2014). Hierarchy formation in newly mixed, group housed sows and management strategies aimed at reducing its impact. *Appl. Anim. Behav. Science.* 160, 1–11. doi: 10.1016/j.applanim.2014.09.011

Hessel, E. F., Reiners, K., and Van den Weghe, H. F. (2006). Socializing piglets before weaning: effects on behavior of lactating sows, pre- and postweaning behavior, and performance of piglets. *J. Anim. Sci.* 84, 2847–2855. doi: 10.2527/jas.2005-606

Janczak, A. M., Pedersen, L. J., and Bakken, M. (2003). Aggression, fearfulness and coping styles in female pigs. *Appl. Anim. Behav. Science.* 81, 13–28. doi: 10.1016/S0168-1591(02)00252-6

Jensen, P. (1980). An ethogram of social interaction patterns in group-housed dry sows. *Appl. Anim. Ethology.* 6, 341–350. doi: 10.1016/0304-3762(80)90134-0

Jensen, P. (1982). An analysis of agonistic interaction patterns in group-housed dry sows - Aggression regulation through an "avoidance order. *Appl. Anim. Ethology.* 9, 47-61. doi: 10.1016/0304-3762(82)90165-1

Jensen, P. (1986). Observations on the maternal behaviour of free-ranging domestic pigs. *Appl. Anim. Behav. Science.* 16, 131–142. doi: 10.1016/0168-1591(86)90105-X

Kanaan, V. T., Lay, D. C., Richert, B. T., and Pajor, E. A. (2012). Increasing the frequency of co-mingling piglets during the lactation period alters the development of social behavior before and after weaning. *J. Appl. Anim. welfare science: JAAWS.* 15, 163–180. doi: 10.1080/10888705.2012.658333

Koolhaas, J. M., Coppens, C. M., de Boer, S. F., Buwalda, B., Meerlo, P., and Timmermans, P. J. A. (2013). The resident-intruder paradigm: A standardized test for aggression, violence and social stress. *J. Visualized Experiments: JoVE.* 4367, 1-7. doi: 10.3791/4367

Kranz, V. A., Horback, K. M., Parsons, T. D., and Pierdon, M. K. (2022). Sow behavior during introduction to a large dynamic group is influenced by familiarity and method. *Appl. Anim. Behav. Science.* 250, 105624. doi: 10.1016/J.APPLANIM.2022.105624

Kutzer, T., Bünger, B., Kjaer, J. B., and Schrader, L. (2009). Effects of early contact between non-littermate piglets and of the complexity of farrowing conditions on social behaviour and weight gain. *Appl. Anim. Behav. Science.* 121, 16–24. doi: 10.1016/j.applanim.2009.08.004

Lenth, R. V., Banfai, B., Bolker, B., Buerkner, P., Giné-Vázquez, I., Hervé, M., et al. (2025). *emmeans: Estimated Marginal Means, aka Least-Squares Means.* Available online at: https://cran.r-project.org/web/packages/emmeans/index.html (Accessed September 12, 2025).

Maes, D., Pluym, L., and Peltoniemi, O. (2016). Impact of group housing of pregnant sows on health. *Porc Health Manage.* 2, 17. doi: 10.1186/s40813-016-0032-3

Marchant-Forde, J. N. (2010). "Aggression and mixing," in *The welfare of pigs* (Springer Science, Brisbane, QLD, Australia), 113–114.

McGlone, J. J. (1985). A quantitative ethogram of aggressive and submissive behaviors in recently regrouped pigs. *J. Anim. science.* 61, 559–565. doi: 10.2527/jas1985.613556

McGlone, J. J. (2013). Updated scientific evidence on the welfare of gestating sows kept in different housing systems. *Prof. Anim. Scientist* . 29, 189–198. doi: 10.15232/S1080-7446(15)30224-2

Morgan, T., Pluske, J., Miller, D., Collins, T., Barnes, A. L., Wemelsfelder, F., et al. (2014). Socialising piglets in lactation positively affects their post-weaning behaviour. *Appl. Anim. Behav. Science.* 158, 23–33. doi: 10.1016/j.applanim.2014.06.001

Norscia, I., Collarini, E., and Cordoni, G. (2021). Anxiety behavior in pigs (Sus scrofa) decreases through affiliation and may anticipate threat. *Front. Vet. Sci.* 8. doi: 10.3389/fvets.2021.630164

O'Connell, N. E., Beattie, V. E., and Moss, B. W. (2003). Influence of social status on the welfare of sows in static and dynamic groups. *Anim. Welfare.* 12, 239–249. doi: 10.1017/S0962728600025665

O'Malley, C. I., Steibel, J. P., Bates, R. O., Ernst, C. W., and Siegford, J. M. (2022). The social life of pigs: changes in affiliative and agonistic behaviors following mixing. *Anim. (Basel).* 12, 206. doi: 10.3390/ani12020206

Oldham, L., Camerlink, I., Arnott, G., Doeschl-Wilson, A., Farish, M., and Turner, S. P. (2020). Winner–loser effects overrule aggressiveness during the early stages of contests between pigs. *Sci. Rep.* 10, 13338. doi: 10.1038/s41598-020-69664-x

Otten, W., Puppe, B., Kanitz, E., Schön, P. C., and Stabenow, B. (2002). Physiological and behavioral effects of different success during social confrontation in pigs with prior dominance experience. *Physiol. Behavior.* 75, 127–133. doi: 10.1016/S0031-9384(01)00630-8

Rault, J.-L. (2012). Friends with benefits: Social support and its relevance for farm animal welfare. *Appl. Anim. Behav. Science.* 136, 1–14. doi: 10.1016/j.applanim.2011.10.002

Rault, J.-L. (2017). Social interaction patterns according to stocking density and time post-mixing in group-housed gestating sows. *Anim. Prod Sci.* 57, 896. doi: 10.1071/AN15415

Razdan, P. (2003). *Stress and early pregnancy in sows: effect on endocrinology, ova transport and embryo development* (Swedish University of Agricultural Sciences, Acta Universitatis Agriculturae Sueciae). Available online at: https://res.slu.se/id/publ/11409 (Accessed March 19, 2025).

R Core Team (2024). *R: A language and environment for statistical computing – Reference Manual* (Vienna: R Foundation for Statistical Computing). Available online at: https://cran.r-project.org/doc/manuals/r-release/fullrefman.pdf (Accessed September 11, 2025).

Rydhmer, L. (2021). "Advances in understanding the genetics of pig behaviour," in *Understanding the behaviour and improving the welfare of pigs (Burleigh Dodds Series in Agricultural Science)*, pp. 3–26. Cambridge, UK: Burleigh Dodds Science Publishing Limited.

Salazar, L. C., Ko, H. L., Yang, C. H., Llonch, L., Manteca, X., Camerlink, I., et al. (2018). Early socialisation as a strategy to increase piglets' social skills in intensive farming conditions. *Appl. Anim. Behav. Science.* 206, 25–31. doi: 10.1016/j.applanim.2018.05.033

Scientific Veterinary Committee (1997). "Scientific Veterinary Committee. (1997). The welfare of intensively kept pigs," in *Report of the Scientific Veterinary Committee, Animal Welfare Section, to the Comission of the European Union*(Brussels, Belgium: European Commission). Doc. XXIV/ScVc/0005/1997.

Stalder, K. J., Karriker, L. V., and Johnson, A. K. (2007).The impact of gestation housing systems on sow longevity.

Stolba, A., and Wood-Gush, D. G. M. (1989). The behaviour of pigs in a semi-natural environment. *Anim. Production.* 48, 419–425. doi: 10.1017/S0003356100040411

Strawford, M. L., Li, Y. Z., and Gonyou, H. W. (2008). The effect of management strategies and parity on the behaviour and physiology of gestating sows housed in an electronic sow feeding system. *Can. J. Anim. Sci.* 88, 559–567. doi: 10.4141/CJAS07114

Sylvén, K. R., Wallgren, T., Almerheim, P., Selling, L. E., Jacobson, M., and Wallgren, P. (2025). A comparison of two systems for group housing of gestating sows - effects on productivity, removal, and treatments. *Porcine Health Management.* 11, 1. doi: 10.1186/s40813-024-00410-9

Taborsky, B. (2021). A positive feedback loop between sociality and social competence. *Ethology* 127, 774–789. doi: 10.1111/eth.13201

Tönepöhl, B., Appel, A. K., Voß, B., König von Borstel, U., and Gauly, M. (2013). Interaction between sows' aggressiveness post mixing and skin lesions recorded several weeks later. *Appl. Anim. Behav. Science.* 144, 108–115. doi: 10.1016/j.applanim.2013.01.004

Turner, S. P., Farnworth, M. J., White, I. M. S., Brotherstone, S., Mendl, M., Knap, P., et al. (2006). The accumulation of skin lesions and their use as a predictor of individual aggressiveness in pigs. *Appl. Anim. Behav. Science.* 96, 245–259. doi: 10.1016/j.applanim.2005.06.009

Turner, S. P., Nevison, I. M., Desire, S., Camerlink, I., Roehe, R., Ison, S. H., et al. (2017). Aggressive behaviour at regrouping is a poor predictor of chronic aggression in stable social groups. *Appl. Anim. Behav. Science.* 191, 98–106. doi: 10.1016/j.applanim.2017.02.002

Turner, S. P., Roehe, R., D'Eath, R. B., Ison, S. H., Farish, M., Jack, M. C., et al. (2009) Genetic validation of postmixing skin injuries in pigs as an indicator of aggressiveness and the relationship with injuries under more stable social conditions1. *J. Anim. Sci.* 87, 3076–3082. doi: 10.2527/jas.2008-1558

Turner, S. P., Roehe, R., Mekkawy, W., Farnworth, M. J., Knap, P. W., and Lawrence, A. B. (2008). Bayesian analysis of genetic associations of skin lesions and behavioural traits to identify genetic components of individual aggressiveness in pigs. *Behav. Genet.* 38, 67–75. doi: 10.1007/s10519-007-9171-2

Turner, S. P., Weller, J. E., Camerlink, I., Arnott, G., Choi, T., Doeschl-Wilson, A., et al. (2020). Play fighting social networks do not predict injuries from later aggression. *Sci. Rep.* 10, 15486. doi: 10.1038/s41598-020-72477-7

van Nieuwamerongen, S. E., Mendl, M., Held, S., Soede, N. M., and Bolhuis, J. E. (2017). Post-weaning social and cognitive performance of piglets raised pre-weaning either in a complex multi-suckling group housing system or in a conventional system with a crated sow. *Anim. Cogn.* 20, 907–921. doi: 10.1007/s10071-017-1110-x

Van Putten, G., and Buré, R. G. (1997). Preparing gilts for group housing by increasing their social skills. *Appl. Anim. Behav. Sci*. 54, 173–183. doi: 10.1016/S0168-1591(97)00063-4

Varela, S. A. M., Teles, M. C., and Oliveira, R. F. (2020). The correlated evolution of social competence and social cognition. *Funct. Ecol.* 34, 332–343. doi: 10.1111/1365-2435.13416

Verdon, M., Hansen, C. F., Rault, J. L., Jongman, E., Hansen, L. U., and Hemsworth, P. H. (2015). Effects of group housing on sow welfare: A review. *J. Anim. Science.* 93, 1999–2017. doi: 10.2527/jas.2014-8742

Wattanakul, W., Stewart, A. H., Edwards, S. A., and English, P. R. (1997). Effects of grouping piglets and changing sow location on suckling behaviour and performance. *Appl. Anim. Behav. Sci.* 55, 21–35. doi: 10.1016/S0168-1591(97)00020-8

Weaver, S. A., and Morris, M. C. (2004). Science, pigs, and politics: A New Zealand perspective on the phase-out of sow stalls. *J. Agric. Environ. Ethics.* 17, 51–66. doi: 10.1023/B:JAGE.0000010844.52041.32

Welfare Quality (2009). "Welfare Quality ® assessment protocol for pigs (sows and piglets, growing and finishing pigs)," in *Lelystad*, The Netherlands: Welfare Quality® Consortium, pp. 1–123.

Weller, J. E., Camerlink, I., Turner, S. P., Farish, M., and Arnott, G. (2019). Socialisation and its effect on play behaviour and aggression in the domestic pig (Sus scrofa). *Sci. Rep.* 9, 4180. doi: 10.1038/s41598-019-40980-1

Weng, R. C., Edwards, S. A., and English, P. R. (1998). Behaviour, social interactions and lesion scores of group-housed sows in relation to floor space allowance. *Appl. Anim. Behav. Science.* 59, 307–316. doi: 10.1016/S0168-1591(97)00143-3

IV

Behavioural Processes 218 (2024) 105042

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Social sham chewing in sows?

Claes Anderson [*], Linda Marie Backeman Hannius, Daiana De Oliveira, Anna Wallenbeck

Department of Animal Environment and Health, Swedish University of Agricultural Sciences, P.O. Box 7068, Uppsala 75007, Sweden

ARTICLE INFO

Keywords:
Pig behaviour
Mixing of sows
Displacement behaviour
Animal welfare

ABSTRACT

In this short communication, we describe chewing behaviour in sows with no apparent edible substrate in their mouth as a potential social behaviour. Chewing in sows during interaction with unfamiliar sows was unexpectedly observed in a study assessing social abilities and damaging behaviours in group-housed dry sows. Such chewing was observed frequently and performed by almost all sows. To our knowledge, this behaviour has not been described previously in a social context in pigs, but rather as an oral stereotypic behaviour related to chronic hunger. We describe the behaviour in its social context and speculate on reasons for its occurrence in that context.

1. Context

This short communication describes a behaviour identified in a larger research project that aimed at developing sustainable and commercially relevant rearing and breeding strategies for sows under group-housing production systems. The experiment and all procedures involved were approved by the National Ethics Committee for Animal Experiments in Uppsala (Registration number: 5.8.18-16279/2017). Within the larger project, we followed 81 sows from birth to second farrowing and investigated effects of additional social mixing. Half of these sows at age 2–5 weeks had access to the neighbouring sows and their litter through a pop hole while the other half did not. From ten weeks of age, half of them were mixed in groups with unfamiliar female pigs, while the other half were kept in intact birth litter groups in a 2 × 2 factorial design. The 81 sows underwent a social interaction test during their second parity [mean age 409.2 days (range 343–470 days)]. The social interaction test consisted in placing a young sow (≤ 2 parities; $n = 81$) and an unfamiliar old sow (> 2 parities, $n = 48$) in a test arena (7.0 m × 5.3 m pen with deep straw bedding) for one hour. Old sows were selected randomly from the sow group that the young sows were about to be merged with. The sows were video-recorded and the frequency and duration of different behaviours were scored using continuous sampling throughout the whole duration of the social interaction test.

2. Sham chewing in a social context

During pilot observations in the one-hour interaction tests, we observed sham chewing occurring during the interaction between young and old sows. To our knowledge this has not been reported previously in the literature in such a social context. The behaviour was analysed in video recordings and if it ceased for at least three seconds and was then initiated again, it was recorded as a new occurrence of the behaviour. Due to its relatively high frequency of occurrence, this response was added to the ethogram as *Sham chewing*. This was defined as chewing, with no apparent substrate in its mouth, often resulting in froth on the sides of the lips of the pig.

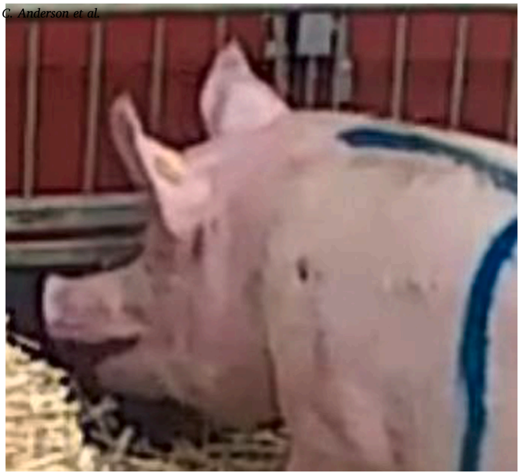
We observed both young and older sows regularly performing such sham chewing during social interactions when they had no food or substrate in the mouth. On several occasions, this behaviour was accompanied by, or resulted in, froth on the sides of the sow's lips. As evidence of the behaviour, we attach a video clip as Supplementary material (see link).

From the total 1 h/sow of video-recording only the first 20 min were analysed in detail. This because most of the social interactions occurred at the beginning of the social interaction test. Young and older sows chewed in 587 and 813 occasions, respectively. All older sows (48/48 old sows) and 95 % of young sows (77/81 young sows) showed this behaviour. Young sham-chewers performed this behaviour significantly less often than older sham-chewers [0.4 ± 0.36 vs 0.6 ± 0.40 counts/min (mean ± SD), T-test: $t = 2.82$, $p = 0.006$]. Time from test start to first sham chewing event was 89.9 ± 169.46 s (range 0.5–1187.9 s) for young sows and 68.1 ± 99.27 s (range 1.9–773.4 s) for older sows (T-test: n.s.). During the test, frequency of sham chewing and social interaction per minutes correlated positively in both young ($r_s = 0.940$, $p < 0.001$) and old sows ($r_s = 0.900$, $p < 0.001$).

---

[*] Corresponding author.
E-mail address: claes.anderson@slu.se (C. Anderson).

https://doi.org/10.1016/j.beproc.2024.105042
Received 4 July 2023; Received in revised form 19 April 2024; Accepted 25 April 2024



Video 1. A video clip is available online. Supplementary material related to this article can be found online at doi:10.1016/j.beproc.2024.105042.

3. How can the occurrence of sham chewing be explained in this context?

To our knowledge, the chewing behaviour we observed in the interactions between a young and unfamiliar older sow, which we describe as *sham chewing*, has previously been described mainly as an oral stereotypic behaviour observed in feed-restricted gestating gilts and sows (e.g. Lawrence and Terlouw, 1993; Stewart et al., 2008; Tatemoto et al., 2019). This has been described as e.g. "*chewing with nothing apparently in mouth*" (Stewart et al., 2008), which is very similar to the behaviour we observed. Previous research describing this as an oral stereotypy attributed it to chronic hunger or inability to perform foraging behaviours (Stewart et al., 2008; D'Eath et al., 2018), to frustration about not being able to forage or as an appetite behaviour without a consummatory phase (Tatemoto et al., 2019). However, all sows in the present study were fed the normal feeding regimen for lactating sows. Additionally, during the social interaction test, sows were kept on deep straw bedding and had opportunities for rooting and foraging behaviours as regularly observed. Thus, the description of stereotypic sham chewing did not fit the context and situation in which our sows were observed. Moreover, sham chewing was only observed during encounters with unfamiliar sows and it is unlikely that an oral stereotypic behaviour, with an underlying cause of hunger or frustration to forage, would have been expressed in almost all sows in such encounters. Sham chewing behaviour may have been expressed in other phases of the larger study, but was only observed by researchers and animal technicians as part of social interactions. It is plausible to think that sham chewing here could be regarded as being related to social interactions between unfamiliar young and old sows.

It can be speculated that sham chewing is a behavioural response associated with some form of communication between sows, possibly a type of agonistic display associated with social hierarchy. Foaming from the mouth has been observed as part of ritualised agonistic behaviours in pigs prior to fights, suggested to be a strategy to avoid costs (Camerlink et al., 2022). In their study, however, foaming was common in the males but "nearly always absent in females", and they suggest that such foaming was a result from repeated teeth grinding, which we did not see in this study. Peden et al. (2018) also suggest that sows use this behaviour to communicate their status in an attempt to avoid physical interaction, which may reduce the risk of injuries. However, a previous study in which sham chewing was considered a stereotypic behaviour found no relationship between social factors, such as aggression (delivered or received) and sham chewing in group-housed nulliparous sows (Hemsworth et al., 2017).

It should be emphasised that social mixing of sows is a stressful event. The sham chewing seen in this study may act as a displacement behaviour in the conflicting situation of whether to attack or retreat. This would explain the high positive correlation between sham chewing and social interactions. Displacement behaviours are frequently associated with frustration, which may explain why sham chewing was performed in a potentially conflicting social situation. A previous study examining displacement behaviours in pigs observed displacement behaviours such as continuous licking of the wall, repeated mastication (i.e. chewing) and salivation (Marcet-Rius et al., 2019). However, the aim of that study was to investigate the effect of straw provision on the behaviour of mini-pigs and observations revealed fewer displacement behaviours (including chewing) in pigs with access to straw. This may indicate that the sham chewing we observed could be considered a displacement behaviour, although the underlying motivation may differ in different situations. If this suggestion is correct, sham chewing behaviour may have relevance for sow welfare, as displacement behaviours can be a result of frustration (e.g. Marcet-Rius et al., 2019).

In future studies on social mixing of pigs, in addition to e.g. counting lesions, we encourage researchers to include sham chewing into the ethogram when measuring social interactions between pigs. Future studies should also investigate the aetiology and underlying motivation for this oral behaviour in this context, to assess its potential usefulness as an animal welfare indicator.

4. In conclusion

In the present article, we describe sham-chewing behaviour in a social context of interaction between unfamiliar individuals. To our knowledge, this has not been reported in the literature before. We encourage researchers studying social interactions in pigs to include these behaviours as part of their ethogram. Future research opportunities could be the aetiology, underlying motivation, and its potential as an animal welfare indicator.

CRediT authorship contribution statement

Anna Wallenbeck: Writing – review & editing, Supervision, Funding acquisition, Formal analysis, Conceptualization. **Daiana De Oliveira:** Writing – review & editing, Supervision, Conceptualization. **Linda Marie Backeman Hannius:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Claes Anderson:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization.

Data availability

Data will be made available on request.

Acknowledgements

Funding for this project was provided by FORMAS, reference no.: 2016-01787.

References

Camerlink, I., Farish, M., Arnott, G., Turner, S.P., 2022. Sexual dimorphism in ritualized agonistic behaviour, fighting ability and contest costs of *Sus scrofa*. Front. Zool. 19, 13. https://doi.org/10.1186/s12983-022-00458-9.

D'Eath, R.B., Jarvis, eBaxter, E.M., Houdijk, J., 2018. Mitigating hunger in pregnant sows. In: Špinka, M. (Ed.), Advances in Pig Welfare. Woodhead Publishing, pp. 199–234. https://doi.org/10.1016/B978-0-08-101012-9.00007-1.

Hemsworth, L., Rault, J.-L., Hemsworth, P., 2017. Sham Chewing and Sow Welfare and Productivity (1C-118). Report prepared for the Co-operative Research Centre for High Integrity Australian Pork.

Lawrence, A., Terlouw, C., 1993. A review of behavioral factors involved in the development and continued performance of stereotypic behavior in pigs. J. Anim. Sci. 71, 2815–2825. https://doi.org/10.2527/1993.71102815x.

Marcet-Rius, M., Kalonjia, G., Cozzib, A., Bienboire-Frosinia, C., Monneretc, P., Kowalczykc, I., Terueld, E., Codecasac, E., Pageat, P., 2019. Effects of straw provision, as environmental enrichment, on behavioural indicators of welfare and emotions in pigs reared in an experimental system. Livest. Sci. 221, 89–94. https://doi.org/10.1016/j.livsci.2019.01.020.

Peden, R.S.E., Turner, S.P., Boyle, L.A., Camerlink, I., 2018. The translation of animal welfare research into practice: the case of mixing aggression between pigs. Appl. Anim. Behav. Sci. 204, 1–9. https://doi.org/10.1016/j.applanim.2018.03.003.

Stewart, C.L., O'Connell, N.E., Boyle, L., 2008. Influence of access to straw provided in racks on the welfare of sows in large dynamic groups. Appl. Anim. Behav. Sci. 112, 235–247. https://doi.org/10.1016/j.applanim.2007.09.006.

Tatemoto, P., Bernardino, T., Alves, L., Zanella, A.J., 2019. Sham-chewing in sows is associated with decreased fear responses in their offspring. Front. Vet. Sci. 6, 390. https://doi.org/10.3389/fvets.2019.00390.

ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

DOCTORAL THESIS NO. 2026:24

Pigs are social animals and group housing supports behavioural needs. However, repeated mixing with unfamiliar individuals can cause aggression and injury. This thesis asked whether genetic predispositions or opportunities to develop social skills could improve their ability to cope with the demands of group housing. Pre-weaning mixing altered behaviours without consistently reducing aggression, whilst post-weaning regrouping may influence injury risk. Genetic line was associated with behavioural patterns and lesion outcomes. Sustainable systems must support sows' capacity to cope with challenges.

Linda Marie Backeman Hannius received her doctoral education at the Department of Applied Animal Science and Welfare at the Swedish University of Agricultural Sciences. She received her Bachelor's and Master's degrees from the Swedish University of Agricultural Sciences.

Acta Universitatis Agriculturae Sueciae presents doctoral theses from the Swedish University of Agricultural Sciences (SLU).

SLU generates knowledge for the sustainable use of biological natural resources. Research, education, extension, as well as environmental monitoring and assessment are used to achieve this goal.

ISSN 1652-6880
ISBN (print version) 978-91-8124-241-6
ISBN (electronic version) 978-91-8124-271-3