INSTITUTE OF GENETICS
AND ANIMAL BIOTECHNOLOGY
of the Polish Academy of Sciences

Exploring social complexity and the benefits of social relationships in domestic pigs

Badanie złożoności społecznej i korzyści płynących z relacji społecznych u świni domowej

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This thesis was submitted to the Institute of Genetics and Animal Biotechnology of the Polish Academy of Sciences in fulfilment of the requirements for the Degree of Doctor in Animal Science

The research for this thesis was conducted at the Animal Behaviour and Welfare Department, Institute of Genetics and Animal Biotechnology of the Polish Academy of Sciences, Jastrzębiec, Poland and at Scotland's Rural College (SRUC), Easter Howgate, UK. The research was conducted within the project titled: **The importance of social relationships and social bonds for animals' behavioural expression, health and fitness – pigs as a model to explore the underlying physiological mechanism**, funded by National Science Centre (NCN), Poland, project number 2020/39/B/NZ8/02508.

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October 2025

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Acknowledgments

I would like to take this opportunity to thank everyone who have directly and indirectly helped in completing the doctoral studies and this dissertation. Thanks to all the research technician, staff at SRUC and at IGBZPAN. My appreciation to Piero Seddaiu for helping with research activities. Special thanks to Patryk Sztandarski for making life at the institute smooth, pleasant and making me feel right at home. My immense gratitude to my supervisors Dr. Irene Camerlink for her continuous support and guidance and Dr. Simon Turner for his valuable insights in making this dissertation whole.

I am grateful to my family for their continuous moral support and motivation in completing this journey.

105 Reviewers
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108 1. **Prof.**
109 2. **Prof.**
110 3. **Prof.**

List of included publications

1. **Khatiwada, S.**, Lee, V., Turner, S.P., Camerlink, I. (2025). Trade-offs between proximity and physical contact during group integration in pigs (*Sus scrofa domesticus*). *Current Zoology.*
   DOI: https://doi.org/10.1093/cz/zoaf056
   Impact factor = 2.1
   Ministry of Education and Science points =100
2. **Khatiwada, S.**, Lee, V., Turner, S.P., Camerlink, I. (2025). Temporal social network structures based on snout contact during group integration in pigs. *Applied Animal Behaviour Science, 292,* 106838.
   DOI: https://doi.org/10.1016/j.applanim.2025.106838
   Impact factor = 2.0
   Ministry of Education and Science points = 100
3. **Khatiwada,** S., Turner, S. P., Farish, M., & Camerlink, I. (2024). Leadership amongst pigs when faced with a novel situation. *Behavioural Processes*, *222*, 105099.
   DOI: https://doi.org/10.1016/j.beproc.2024.105099
   Impact factor = 1.5
   Ministry of Education and Science points = 70
4. **Khatiwada, S.,** Seddaiu, P., Jaszczyk, A. & Camerlink, I. (2025). Is social support mediated by social relationship strength in pigs? *Animal*
   Doi: https://doi.org/10.1016/j.animal.2025.101693
   Impact factor = 4.2
   Ministry of Education and Science points = 200

Summary

Understanding the potential drivers of social behaviour is important for interpreting how social organisation and dynamics develop among group-living animals. It is also necessary to consider both the causes and consequences of social behaviour to improve the conditions in which animals are kept. Each species, and even each group may show different patterns of social organisation, some more complex than others. Social traits such as eusociality, cooperative structures, and dominance hierarchies help explain the diversity of social systems in animals.

This dissertation focuses on the behavioural processes of young domestic pigs, which typically form dominance hierarchies. It explores various factors that influence social behaviour, particularly those related to maintaining social relationships. These behavioural patterns and their implications may offer insights into how young animals interact within a structured social group. Considerable research effort has focused on the role of overt agonistic behaviour in the establishment and maintenance of social relationships in species that adopt a dominance hierarchy. Much less effort has been directed at exploring the role of subtle, affiliative or neutral forms of interaction, which this thesis focused on. Behavioural data were collected through live observation and video recordings across different experimental settings and were analysed using approaches such as mixed modelling, permutation tests and social network analysis. Across a series of publications, the study reports on patterns of behaviour related to recognition and the transmission of social information, as well as the expression of leadership and the potential benefits of social relationships.

The findings show that subtle social behaviours may have different implications, whereby snout proximity was most common during periods of social instability and declined as stability increased, while snout contact remained relatively stable. Pigs that engaged more in snout proximity tended to grow more slowly, whereas those that initiated or received more snout contact showed a better growth performance. This may suggest that slower growing individuals, who may be more vulnerable, used snout proximity as a strategy to avoid direct contact during unstable periods. As group integration progressed, pigs interacted with fewer partners, but the frequency of snout contact with those partners increased. No evidence was found for consistent social preferences or centralised associations. Pigs showed more snout contact with non-siblings than

with siblings, and with individuals who had different early-life experiences. Males initiated contact more often, while females occupied more central positions in the social network.

Leadership behaviour was also examined and found to be only marginally consistent in pigs. Females were more likely than males to take on leadership roles, in line with their social structure in nature, but body weight and coping style did not appear to influence this. The benefits of social relationships were assessed through a social support test. Pigs paired with a sibling with whom they had a strong relationship (interacted with frequently) showed shorter and less frequent snout and head proximity and produced more low-pitched vocalisations. Cortisol levels increased following the stressful event, but no significant differences were found between groups with strong or weak social relationships. Most companions remained calm, though their contact seeking behaviour varied. Female companions differed from males in how they responded. Overall, the results suggest that relationship strength may influence behavioural responses to stress, even if not reflected in hormonal measures.

In general, the study highlights the importance of examining subtle behaviours, particularly those involved in recognition and information exchange, as these may serve functions related to affiliative care. Non-agonistic behaviours such as snout contact appear to play a key role in the social dynamics of pigs. Although the study focused on domestic pigs, some behavioural traits observed, such as female leadership, reflect those seen in wild populations, where females often lead despite males being physically dominant. The parallels between the behaviour of domestic and wild pig populations shows the continued relevance of studying natural behaviour, and social behaviour in particular. The findings suggest that social relationships among pigs are complex, and that close companionship may help animals cope with stress. In summary, the behavioural expressions, leadership traits, social benefits as well as the methods used to explore these social dynamics in this study contribute to a broader understanding of social complexity in group-living animals.

Streszczenie

Zrozumienie potencjalnych czynników kształtujących zachowania społeczne jest kluczowe dla interpretacji sposobów, w jakie organizacja oraz dynamika społeczna rozwijają się w grupowo żyjących populacjach zwierząt. Istotne znaczenie ma również uwzględnianie zarówno przyczyn, jak i konsekwencji zachowań społecznych, co umożliwia optymalizację warunków utrzymania zwierząt w środowisku hodowlanym lub badawczym. Poszczególne gatunki, a nawet odmienne grupy w obrębie jednego gatunku, mogą prezentować zróżnicowane wzorce organizacji społecznej, których stopień złożoności jest zmienny. Właściwości takie jak eusocjalność, struktury kooperacyjne, czy hierarchie dominacji stanowią istotne elementy wyjaśniające szerokie spektrum systemów społecznych obserwowanych u zwierząt.

Niniejsza rozprawa koncentruje się na analizie procesów behawioralnych młodych świń domowych, które zazwyczaj tworzą hierarchie dominacji. Praca bada zróżnicowane czynniki wpływające na zachowania społeczne, ze szczególnym uwzględnieniem mechanizmów utrzymywania relacji społecznych. Opisywane wzorce zachowań oraz ich implikacje dostarczają cennych informacji na temat sposobów, w jakie młode osobniki wchodzą w interakcje w obrębie zorganizowanej grupy społecznej. Dotychczasowe badania koncentrowały się głównie na roli jawnych zachowań agonistycznych w nawiązywaniu i podtrzymywaniu relacji społecznych u gatunków charakteryzujących się hierarchiczną strukturą dominacji. Zdecydowanie mniej uwagi poświęcono natomiast subtelnym, afiliacyjnym i neutralnym formom interakcji, które stanowią zasadniczy przedmiot niniejszej pracy. Dane behawioralne zebrano poprzez obserwację na żywo i nagrania wideo w różnych warunkach eksperymentalnych, a następnie przeanalizowano przy użyciu takich metod jak: modelowanie mieszane, testy permutacji i analiza sieci społecznych.

W serii publikacji przygotowanych w ramach niniejszego badania przedstawiono wzorce zachowań związanych z rozpoznawaniem oraz przekazywaniem informacji społecznych, a także z manifestowaniem przywództwa i potencjalnymi korzyściami wynikającymi z relacji społecznych u świń. Uzyskane wyniki wskazują, że subtelne interakcje społeczne mogą pociągać za sobą zróżnicowane konsekwencje. Bliskość pyska okazała się najczęściej obserwowanym zachowaniem w okresach niestabilności społecznej, po czym jej częstość malała wraz ze wzrostem stabilności grupy. Jednocześnie kontakt pyska pozostawał relatywnie stabilny w czasie. Zaobserwowano, że osobniki częściej angażujące się w zachowanie polegające na utrzymywaniu bliskości pyska charakteryzowały się wolniejszym tempem wzrostu. Natomiast świnie inicjujące

lub otrzymujące większą liczbę kontaktów pyskiem wykazywały lepsze wskaźniki wzrostu. Wyniki te sugerują, że wolniej rosnące, prawdopodobnie bardziej wrażliwe osobniki mogą wykorzystywać bliskość pyska jako strategię redukcji ryzyka bezpośredniej konfrontacji w okresach destabilizacji struktury społecznej. W miarę postępu procesu integracji grupowej zmniejszała się liczba partnerów społecznych, z którymi zwierzęta wchodziły w interakcje. Jednocześnie rosła częstotliwość kontaktów pyskiem z tymi, którzy pozostawali kluczowymi partnerami. Nie uzyskano dowodów potwierdzających występowanie stałych preferencji społecznych ani scentralizowanych skojarzeń pomiędzy osobnikami. Zaobserwowano ponadto większą liczbę kontaktów pyskiem z osobnikami niespokrewnionymi w porównaniu z rodzeństwem oraz z osobnikami, które doświadczały odmiennych warunków środowiskowych we wczesnym okresie życia. Samce inicjowały kontakty społeczne częściej, natomiast samice zajmowały bardziej centralne pozycje w strukturze sieci społecznej.

Zbadano również zachowania związane z przywództwem, przy czym wyniki wskazują, że cecha ta wykazuje jedynie marginalną spójność u świń domowych. Samice częściej niż samce podejmowały role przywódcze, co pozostaje zgodne z naturalną strukturą społeczną tego gatunku. Masa ciała oraz indywidualny styl radzenia sobie ze stresem nie wykazały istotnego wpływu na pełnienie funkcji przywódczych. Potencjalne korzyści wynikające z relacji społecznych oceniano za pomocą testu wsparcia społecznego. Świnie dobrane z rodzeństwem, z którym łączyła je silna więź (rozumiana jako wysoka częstość dobrowolnych interakcji), charakteryzowały się krótszym dystansem pyska i głowy od osobnika, rzadszym oddalaniem się oraz częstszą wokalizacją o niskiej częstotliwości. Poziom kortyzolu wzrastał po stresorze u wszystkich grup, jednak nie ujawniono istotnych różnic między osobnikami utrzymującymi silne oraz słabe relacje społeczne. Większość towarzyszących osobników zachowywała względny spokój, choć obserwowano zróżnicowanie w zachowaniach ukierunkowanych na poszukiwanie kontaktu. Reakcje samic różniły się przy tym od reakcji samców. Uzyskane wyniki wskazują, że siła więzi społecznych może modulować behawioralne reakcje na stres, nawet jeśli nie znajduje to jednoznacznego odzwierciedlenia w markerach endokrynnych.

Podsumowując, przeprowadzone badanie podkreśla konieczność szczegółowej analizy subtelnych zachowań społecznych, zwłaszcza tych związanych z rozpoznawaniem oraz wymianą informacji, ponieważ mogą one pełnić istotne funkcje afiliacyjne. Zachowania nieagonistyczne,

takie jak kontakt pyskiem, odgrywają kluczową rolę w kształtowaniu dynamiki społecznej świń domowych. Chociaż analizy przeprowadzono na populacji świń udomowionych, część zaobserwowanych tendencji behawioralnych, między innymi częstsze pełnienie ról przywódczych przez samice, znajduje odzwierciedlenie również w populacjach dzikich. W środowisku naturalnym samice często przewodzą grupom, mimo że samce cechują się przewagą fizyczną. Zbieżność tych obserwacji wskazuje na niezmienne znaczenie badań nad zachowaniami naturalnymi, a w szczególności nad aspektami społecznymi funkcjonowania gatunku. Wyniki sugerują, że relacje społeczne między osobnikami cechują się wysokim stopniem złożoności, a bliskie towarzystwo może pełnić funkcję ochronną poprzez łagodzenie reakcji stresowych. Podsumowując, uzyskane dane dotyczące ekspresji behawioralnych, cech przywódczych oraz korzyści społecznych, jak również zastosowane metody analityczne, wnoszą istotny wkład w szersze zrozumienie złożoności struktur społecznych u zwierząt żyjących w grupie.

1. Introduction

Mammalian societies are shaped by their social structures and interactions, which have led to the development of various behavioural systems such as eusociality, kinship-based organisation, and hierarchical groupings (Hamilton, 1971; Silk, 2002). Maynard-Smith and Szathmáry (1995) suggested that the emergence of complex social systems represents a major evolutionary milestone. Social complexity, together with other behavioural processes, has been described through cooperative behaviour, reproductive suppression, dominance hierarchies, and kinship structures (Kappeler et al., 2019; Hobson et al., 2019). Some researchers have distinguished between organisational complexity, which is more evident when kinship levels are high (Hamilton, 1971; Silk, 2002), and relational complexity, which becomes relevant when kinship is low (Silk, 2006; Seyfarth and Cheney, 2012).

The lack of consistent social processes may reflect the diversity of functions underlying interactions, and the variation in interaction patterns, behavioural expressions, and their outcomes, which together shape the unique social organisation of each animal society. For instance, female philopatry is common in non-human primates (Sterck et al., 1997) and lion social units (Pusey and Packer, 1987), but although centred around female cooperation, the social group may be temporarily led by males who guide the group to new foraging/hunting areas or defend territory. These examples suggest that social structures, dynamics, and complexity are shaped by the sum of behavioural processes and their consequences, with each species exhibiting a distinct set of traits that characterise its social system.

Behaviours that support individual recognition and the exchange of social information can offer benefits, although they may also carry risks. Despite this, animals continue to express such behaviours, as they are essential for forming associations, engaging in interactions, and maintaining relationships (Hinde, 1976; Grueter et al., 2020). Exposure to risk or novelty can influence how group-living animals organise themselves. Therefore, aspects such as behavioural expression, patterns of association, and responses to risk or novelty (such as leadership) are central to understanding social organisation and complexity in animals that live in groups. Additionally, the nature of relationships between individuals plays a key role in shaping group dynamics.

This study aims to explore three key aspects of social behaviour, (i) behavioural expressions linked to the transmission of social information and recognition of conspecifics, particularly during group integration, (ii) leadership as a behavioural trait, which plays a role in group survival, movement, and resource exploration, and (iii) the impact of social relationships on individual outcomes, specifically whether individuals with stronger social bonds experience greater benefits than those with weaker relationships. These areas help to better understand the social dynamics and organisation within groups.

This was studied in domestic pigs (*Sus scrofa domesticus*) as they are a versatile and relevant research model with translational value to both human and natural sciences (e.g. Vodička et al., 2005). Their social structure (dominance hierarchies) and social behavioural repertoire allow us to test the hypotheses in a controlled setting on a large number of replicates. Importantly, pigs show a rich array of social behaviours and have preferential social relationships (Durrell et al., 2004; Goumon et al., 2020; Clouard et al., 2024). Moreover, identifying the role of positive social interactions will form an important component to address fundamental knowledge gaps, e.g. how different positive social behaviours interact. Studies indicate that in pigs, their social behaviour has an impact on their growth performance (Camerlink et al., 2012) and immunity (De Groot et al., 2001). Pigs respond strongly to social isolation and social stress, with consequences for their behaviour, neurobiology and immune response (Ruis et al., 2001; Kanitz et al., 2004; Gimsa et al., 2018). They respond to each other's emotional state, i.e. social contagion (Reimert et al., 2015); offer social support to a distressed conspecific (Rault, 2012; Reimert et al., 2014); and respond positively to social contact from conspecifics (e.g. Reimert et al., 2015) and humans (Lürzel et al., 2020). Moreover, social contact elicits an oxytocin response in pigs that can be measured from saliva (Lürzel et al., 2020). Pigs' reproductive performance, and thus fitness, is negatively affected by social stress (Von Borell et al., 2007) which has a negative impact on the subsequent performance of the offspring, thus further reducing fitness (Rutherford et al., 2014). However, it is unknown whether positive social interactions create the opposite, beneficial, effect on fitness.

Snout contact is a biologically relevant behaviour in pigs, known to strengthen the bond between the sow and her offspring (Newberry et al., 1988; Blackshaw and Hagelsø, 1990; Petersen et al., 1990). Previous studies have linked receiving contact, regardless of whether it involves snout proximity or direct contact, with improved growth performance (Camerlink et al., 2012; Camerlink

and Turner, 2013). Snout-to-body contact, which in some studies include nudging or snout-to-snout interaction, has also been identified as a marker of play (Horback, 2023), while snout proximity is thought to support social recognition (Penn and Frommen, 2010). Pigs use olfactory cues to distinguish familiar from unfamiliar individuals, which requires close interaction (Kristensen et al., 2001; Schild and Rørvang, 2023). Given that pigs maintain dominance hierarchies, often through agonistic behaviour that can escalate into fights (Clark and D'Eath, 2013; Camerlink et al., 2022), individuals would aim to avoid direct contact with unfamiliar conspecifics to minimise risk, as animals tend to make decisions that optimise outcomes (Bogacz, 2007). Considering the multiple roles that snout contacts play in pig social organisation, it is important to investigate both its benefits and the patterns of association it reflects.

Leadership is another trait relevant to group survival, movement, and resource discovery, yet it has received limited attention in pigs. Early work dates back to Meese and Ewbank (1973a), but the topic has not been widely explored since. Leadership involves being the first to act, whether initiating movement, performing a task, or recruiting others (Fischhoff et al., 2007; King et al., 2008; Peterson et al., 2002). It is often linked to other behavioural expressions such as personality (Kurvers et al., 2009; Harcourt et al., 2009) and food exploration (Beauchamp, 2000; Schuett and Dall, 2009). Leadership tends to be expressed by individuals with specific characteristics, including familiarity with their environment, motivation to act, and a tendency to exert influence or dominance (Boinski and Garber, 2000; King et al., 2009). Studying leadership in pigs can therefore provide further insight into their social structure.

Maintaining social relationships can offer various benefits to animals, including improved birth rates and higher infant survival (McFarland et al., 2017), as well as better thermoregulation (McFarland et al., 2015). In addition to immediate fitness benefits, strong social bonds can provide social support, including social buffering, which helps protect individuals from the negative effects of stress (Cohen and Wills, 1985). Social support has been documented across a range of species (Massen et al., 2010), including several farm animals (Rault, 2012), and has been shown to reduce stress responses in social partners (Meehan et al., 2017; Wittig et al., 2016; Færevik et al., 2006). The effectiveness of social support may depend on the nature of the relationship between individuals (Yang et al., 2016; Silk et al., 2010), and may also reflect the influence of kinship,

353 which is considered one of the strongest factors shaping social relationships in animals (Lukas and
354 Clutton-Brock, 2018).

355 Together, understanding the effect of positive or neutral forms of behavioural expression,
356 social associations, and the outcomes of social relationships, is important to build a clearer
357 understanding of social structure and group dynamics. The insights gained from this research can
358 contribute to improving animal welfare and management practices in domestic animals and offer
359 a deeper understanding of the causes and consequences of social behaviour across wild and
360 domestic animal populations.

361

2. Hypotheses

Publication 1

1. Individuals choose non-tactile over tactile behaviour when risks are high. Prediction: We predict more non-tactile snout proximity, and little tactile behaviour, in the early stage of group integration when there is frequent aggressive behaviour, but more tactile snout contact and less non-tactile proximity when groups are more socially stable, as evidenced through low aggression.
2. Individuals derive benefits from tactile contact. Prediction: The subtle differences in social behaviour (contact versus proximity) can have opposite outcomes for animal health.

Publication 2

3. Social networks based on snout contact change over time as group integration progresses. Prediction: Pigs initially show cluster formation based on individual familiarity, while over time group cohesion increases and social preferences start to form.

Publication 3

4. Pigs show leadership when the social group is challenged with a potential threat. Prediction: Within a social group only few individuals will show leadership traits whereas the rest are followers.
5. Leadership is related to individual traits such as body weight and coping strategy. Prediction: Proactive and heavier individuals have a greater likelihood of adopting a leadership role, as such individuals would theoretically suffer less from taking a risky behavioural strategy.

Publication 4

6. The strength of a social relationship influences pigs' behavioural response in an anxiogenic situation. Prediction: Individuals paired with a partner that they have a strong relationship with show less stress-related behaviour.
7. Individuals from dyads with a strong social relationship show a reduced physiological response in each other's presence. Prediction: The cortisol concentration in individuals with a strong relationship would be less than in the individuals with a weak relationship.

3. Objectives

Publication 1

1. The aim of the study was to investigate the occurrence of snout proximity and snout contact during social encounters in pigs, while exploring the benefits individuals may derive from these behaviours.

Publication 2

2. The aim of this study was to investigate how pigs re-establish their social relationships, including social preferences, after a regrouping event, and the association pattern of subtle social interactions within this context.

Publication 3

3. The aim of this study was to investigate the occurrence of leadership and factors related to leadership in domestic pigs during a potentially stressful event.

Publication 4

4. The aim of this study was to investigate whether the behavioural and physiological responses of pigs exposed to a stressor are influenced by the strength of the social relationship to the partner present during the event.

4. Material and methods

The thesis includes the experimental procedures from three different experiments. Publication 1 and 2 are based on a study conducted in 2022-2023 at the pig research farm of SRUC, in the UK. Publication 3 is based on data available from SRUC. Publication 4 is from data collected at the IGBZPAN, Poland, from 2022-2024. Hence, the animal and housing section is reported separately for each publication.

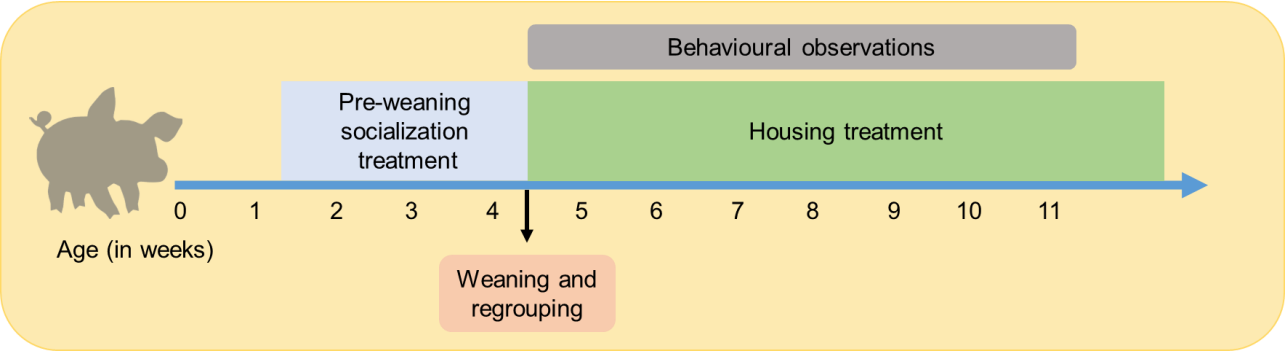
4.1 Animals and housing

4.1.1 Publication 1-2

This observational study was performed at the Easter Howgate pig unit of Scotland's Rural college (SRUC), Easter Howgate, UK. The experiment was adhering to the guidelines approved by SRUC's Animal Experiments Committee and was authorised by the UK Home Office (Project Licence: PP1403242). In total 142 pigs (72 males and 70 females) were studied. The pigs were a crossbred from Large White × Landrace sows and Danish Duroc boars. The study involved 18 groups across three batches for the data reported in publication 1 and 15 groups for the data of publication 2. For both trials, the behavioural observations related to this thesis started when the pigs were four weeks old. About half of the piglets, aged 10-14 days, were socialised (referred to as SOC treatment) before weaning by allowing interaction between two litter groups through an opening between farrowing pens, while the sows remained separated. At four weeks, the pigs were weaned and moved to a different research building where new groups were formed by combining different sibling groups (**Figure 1**). Each group consisted of eight pigs; four pigs from each of two different litters. Each pig was therefore housed with three familiar and four unfamiliar pigs. Although the number of socialised pigs per group was balanced as much as possible, six groups did not contain socialized pigs due to variation in the date of birth. The pigs in the new groups did not know each other from pre-weaning socialization. The groups were housed either in enriched housing conditions (referred to as ENR; 9 pens of 6.9 m × 2.1 m with deep straw bedding, Porcichew pig toys, and hessian ropes) or less-enriched conditions (referred to as control, CON; 9 pens of 4.6 m × 2.1 m with rubber mats and wood shavings but no straw or toys). All pigs within a group were exposed to the same housing condition, and sibling groups were balanced across

446 housing conditions. The lights were on from 07:00 to 19:00, and the room received natural daylight
447 through windows. The pigs were fed commercial pig feed *ad libitum* and had access to water via
448 nipple drinkers. They were weighed regularly, and average daily weight gain (ADWG) in kg per
449 day was calculated for weeks 4-5, 6-8, and 10-11, using the formula ADWG = (weight last week
450 - weight first week) / days between weeks. For individual identification, pigs were ear-tagged and
451 marked with animal marker spray on their backs. During the observation period, three out of 142
452 pigs were removed from the study due to health issues.

453



454

455 **Figure 1.** A schematic representation of experimental treatments and events by age of the pigs
456 (publication 1-2).

457

458 *4.1.2 Publication 3*

459 A dataset was used for which the experiment was conducted by other researchers in 2014
460 at the Easter Howgate Pig unit of SRUC, Easter Howgate, UK. The SRUC's Animal Ethics
461 Committee and the UK Government Home Office (Project licence PPL60/4330) approved the
462 experimental protocol (no. ED AE 21–2014). Male (n=184) and female (n=182) domestic pigs,
463 which were a crossbreed of Large White × Landrace sows, and American Hampshire boars, were
464 studied from 53 litters across four farrowing groups. The piglets were raised in pens with sows in
465 farrowing crates. Piglets were weighed, vaccinated, and tagged for identification at birth with tails
466 and teeth kept intact, and males were raised without castration. The piglets were weaned at ~28
467 days old and allowed to stay in the farrowing pen for an additional week. The average weaning

weight was 7.98 ± 1.41 kg (mean ± SD) for males (range 3.7–12 kg) and 7.66 ± 1.48 kg (mean ± SD) for females (range 3–11.4 kg).

At 5 weeks of age, the pigs were moved to a research facility while remaining within their original sibling groups. Each group averaged 12 ± 2 pigs. The pens, measuring 1.9 m × 5.8 m (11 m^2), had solid floors with deep straw bedding, providing 1.0–1.1 m^2 per pig. In winter, a straw-covered kennel area was available to maintain a suitable ambient temperature for the pigs. Each pen had a single-space feeder and a drinker, with unlimited access to commercial pelleted feed and water. The lights were on from 07:00 to 19:00, and the room received natural daylight through windows.

4.1.3 Publication 4

In total 68 pigs participated in the study, of which 34 were focal animals. Three pigs were removed from the analyses due to an inconsistency in the test set-up or missing samples, therefore, n = 31 focal pigs for analyses. Pigs were from the Puławska breed and were studied at on average 16 weeks of age (4 months; range 15-18 weeks). Focal animals were females (gilts) while the support companion pig was a male (uncastrated male; n = 24) or female (n = 10) depending on the available pigs within the research criteria. Pigs were born in free farrowing pens and kept together as a litter without cross-fostering. They were weaned between 4 and 5 weeks of age. From 6 weeks of age, pigs were assigned to enriched or barren housing conditions, which was part of an overarching research question. All pigs were housed in a 6 m^2 pen (2 × 3m) with a solid floor. Barren housed pigs had two static enrichment items (metal chain and sisal rope hanging from the wall) and no substrate. Enriched housed pigs had straw bedding and received each week a novel object and a fresh manipulable object for the duration of the study. Pens were cleaned every other day and the enriched pens received fresh straw after cleaning. Pigs received *ad libitum* commercial pig feed suitable to their weight category and had *ad libitum* access to water.

From 6 weeks of age, litters with more than five pigs were randomly divided into two separate groups and remained in this group composition until the test. This created variation in relationship strength, whereby some siblings were continuously housed together for 16 weeks whereas other siblings were housed together only for the first 6 weeks of life and not for the

remaining 10 weeks. This difference in relationship strength between siblings formed the contrast (treatment) for the social support test.

4.2 Experimental setup

4.2.1 Behavioural observations (Publication 1-2)

The behaviours of snout proximity, snout contact, and aggressive behaviour were observed based on the ethogram in **Table 1**, noting both the initiator and recipient. Observations were conducted from week 4 to week 11 (excluding week 9) using continuous live and video sampling. Live observations were conducted by standing at a distance of the pen to not disturb the groups (**Figure 2**). Some observations were done from video to obtain a wider range of hours per day (07:00 – 18:00). Each group was observed for 15 minutes per session, with 3-4 sessions daily, resulting in 45 minutes to 1 hour of observation per group each day. Each week included two observation days (except for week 4, which had three days), leading to 2 hours of observation per group weekly. Over seven weeks, this amounted to approximately 14 hours of observation per group. A single observer recorded the behaviours using the "Animal Behaviour pro" application (Newton-Fisher, 2021) on an iPad mini 2.

Table 1. Ethogram of observed behaviours in 4-11 weeks old pigs (n = 142).

Behaviour	**Description**
Snout proximity	Pig proactively brings its snout within 30 cm distance of the snout of another pig, by turning its head towards the other, without making contact (irrespective of the duration).
Snout contact	Pig proactively touches the snout (area below the eyes, including nose disc) of another pig with its nose disc (irrespective of the duration).
Aggression	Pig delivers a head knock, threat, push and/or bite to another pig, or engages in a mutual fight, including a rapid sequence of biting. Can include moments in which the opponents stand still (pause) to regain breath. Continues until one retreat or until other behaviour (excl. standing still) is performed for at least 3 s.

Research suggests that pigs experience a peak in aggression immediately after regrouping, which then gradually declines over the following three weeks (Meese and Ewbank, 1973b;

Prevolnik et al., 2021). Consequently, data were combined across several weeks such that social stability was categorized into three phases: weeks 4-5 (equivalent to weeks 1-2 post-regrouping) represent a period of low social stability, weeks 6-8 (weeks 3-5 post-regrouping) indicate moderate social stability, and weeks 10-11 (weeks 7-8 post-regrouping) reflect high social stability. Behavioural observations and average daily weight gain (ADWG) data were segmented according to these phases: low (weeks 4-5), medium (weeks 6-8), and high (weeks 10-11). These classifications were determined based on aggression levels, with the highest aggression occurring in the initial two weeks after regrouping, followed by a decline in subsequent weeks.

Figure 2. Example of the setup for observing snout contact and snout proximity behaviour (for Publication 1-2).

4.2.2 Dominance relationships (Publication 1)

From the overall frequency of aggressive interactions, the Modified David Score (MDS) was calculated as an indicator of dominance rank. The Modified David Score is an adaptation of the original David's Score, which is a method used to rank individuals in a social group based on their dominance interactions. The MDS was calculated using the "steepness" package" (version 0.3-0) (Leiva and de Vries, 2022) in R (version 4.3.2) (R Core Team, 2023). Due to the relatively infrequent occurrence of aggression in some weeks, dominance relationships could not be calculated by week to show the change over time but were instead calculated across the whole observation period.

4.2.3 Backtest (Publication 3)

The backtest is a widely used behavioural assessment in piglets to determine their coping styles (e.g. Zebunke et al., 2017). A total of 366 piglets underwent this test, following the methodology established by Hessing et al. (1993) and described by Melotti et al. (2011). The test was conducted when the piglets were an average age of 15.4 ± 1.02 days (range 13-18 days). Each litter was moved to a room next to the testing area. The order of testing was balanced across litters from primiparous and multiparous sows (n = 14 and 20, respectively). The experimenter randomly selected a piglet and brought it to the test room. The piglet was placed on its back on a 25 kg feed bag positioned on a table, which had a slight indentation to support its spine, and was held in this position for one minute. The experimenter held the piglet's thorax with one hand, securing one foreleg between the thumb and index finger and the other foreleg between the index and middle finger. The other hand was placed loosely on the hind legs (Bolhuis et al., 2003). The handler recorded the number of resistance attempts (i.e., struggles), defined as body or leg movements due to muscle tension that continued until the piglet relaxed its hind legs for at least one second. Another observer counted the number of vocalizations, with each breath producing a distinct sound counted as one instance. The piglet was weighed and returned to the sow. Frequent struggles and vocalizations indicate a proactive coping style (Spake et al., 2012), whereas immobility and silence suggest a reactive coping response. Vocalization counts ranged from 0 to 64 (median 8), while struggle counts varied from 0 to 8 (median 1), demonstrating adequate variability for analysis. The distribution of these behaviours was skewed, with 24% (n = 95) of piglets remaining silent and 29% (n = 114) not struggling.

559 *4.2.4 Human Approach Test (HAT) (Publication 3)*

560 The Human Approach Test (HAT) has been utilized to evaluate pigs' reactions to humans,
561 particularly their fear response (Leliveld et al., 2017; Désiré et al., 2023). A total of 366 pigs (from
562 32 groups) were tested at six weeks of age, a stage when their interactions with humans were
563 limited to routine farm care and the backtest. The test was conducted three times over a seven-day
564 period, on three separate afternoons (Thursday, Friday, and Monday), with the order of testing
565 balanced among the groups. To ensure individual recognition, pigs were marked on their backs
566 using animal marker spray, applied either the day before or on the morning of the test. All tests
567 were conducted by one person, referred to as the 'experimenter.' The experimenter had no prior
568 familiarity with the pigs and wore a red overall to distinguish themselves from the farm staff, who
569 wore blue overalls. Upon entering the experimental pen (different from the home pen), the
570 experimenter moved slowly along the walls to ensure all pigs were awake and attentive. She then
571 positioned herself at the centre of the wall opposite the entrance, standing still with her back against
572 the pen wall. A half-circle with a 0.5-meter radius, marked with blue spray paint, was drawn on
573 the floor around the experimenter. This position was maintained for ten minutes. During the test,
574 the experimenter recorded the time (in seconds) it took for each pig to approach within the 0.5-
575 meter radius with either its head or forelimbs, as well as the time taken to make physical contact.
576 If a pig did not enter the marked radius within the ten-minute period, it was assigned a latency time
577 of 600 seconds. The tests were also recorded using CCTV cameras mounted on the ceiling,
578 allowing for later analysis of the pigs' behaviour.

579 *4.2.5 Assignment of leadership (Publication 3)*

580 In each group, leadership was assigned to the first pig that contacted the experimenter
581 during the HAT. If multiple pigs touched the experimenter simultaneously, all were designated as
582 leaders. If no pig made contact, no leader was assigned. Pigs that maintained a leadership role
583 across all three test days were classified as "consistent leaders" while those that led on only some
584 occasions were labelled as "inconsistent leaders". The remaining pigs were categorized as
585 followers. A leader was identified for each test day, and any role changes (leader or follower) were
586 recorded. The three repeated observations per pig were used to assess the repeatability of
587 leadership. To determine factors predicting leadership, the analysis focused on the first test where
588 a leader emerged. Groups were classified as having a "distinct leader" if only one pig assumed the

589 role, rather than multiple pigs touching the experimenter at the same time. As a result, individual-
590 level data indicated whether a pig was a consistent leader, an inconsistent leader, or a follower on
591 each test day, while group-level data determined whether a group had a distinct leader (either
592 consistent or inconsistent) on each test day.

593 *4.2.6 Social support test (Publication 4)*

594 The 34 focal pigs were tested across five batches (i.e. cohorts) in a social support test based
595 on Reimert et al. (2014). However, based on a pilot study, the test duration was reduced from 15
596 to 4 minutes as a refinement to the procedures, to remain below the endpoints set for the ethical
597 treatment of animals. Due to regular cognitive tests as part of the overarching project, all animals
598 were accustomed to human handling and trained to go into the test room alone for at least 5
599 minutes, which was previously associated with a food reward. Therefore, all pigs were well
600 habituated to the test room whereas being in the weigh crate was expected to constitute a
601 stressor. The test room was 3.5 × 3.5 m with solid walls and one entry gate. A metal weigh crate
602 (dimensions in l × w × h: 122 × 60 × 60 cm in batch 1 and 145 × 53 × 85 cm in other batches) was
603 placed in the centre of the room, facing a wall (**Figure 3**). The tiled floor was bedded with a small
604 layer of straw (without straw in the crate). The focal pig was led from the home pen to the test
605 room (ca. 30 m distance) and led into the weigh crate. The test was started, and the focal pig
606 remained for 1 minute on their own in the test room (with the aim to arouse a mild stress), here
607 referred to as the solitary phase. After 1 minute, a companion pig was brought into the test room
608 for social support, starting the social phase (**Figure 3**). The companion was either a sibling from
609 the same social group (a pen-mate) as the focal pig (strong relationship) or a sibling from another
610 group (weak relationship), which formed the main treatment. Where possible, the selected
611 companion was a male with lower body weight than the focal pig to avoid dominance threats to
612 the focal animal. Due to an uneven sex distribution in the population, 24 companions were male
613 (15 strong; 9 weak treatment) and 10 were female (5 strong; 5 weak). Companions were only used
614 once in the test and never tested as the focal pig. The companion was free to walk around in the
615 test arena and could interact with the focal pig through the bars of the weigh crate. At 3 minutes
616 after the entry of the companion the test was ended and both pigs were returned to their home pen.
617 The test arena was cleaned in between tests. Dyads of each treatment were balanced across the day
618 (10:00 – 16:00) to avoid a confound between daytime and treatment. Endpoints that were set to

terminate the test early in case of excessive stress responses (escape attempts or hyperventilation) were not reached.

Figure 3. Layout for social support test without companion (solitary phase) and in the presence of a companion (social phase).

4.2.7 Social differentiation test (Publication 4)

To verify whether the focal pigs still recognized their former pen mates (either based on familiarity or kin recognition; Stookey and Gonyou, 1998), and whether they distinguished them from completely unfamiliar pigs, they were observed in a regrouping situation. The day after the social support test, all focal pigs (within a batch) were grouped together with at least one sibling from their home pen, one sibling from a different pen, and an unfamiliar pig of the same age (no sibling or pen mate). This resulted in groups of 13-14 pigs. Pigs were marked with an animal marker crayon for individual recognition. The regrouping arena was 12 m^2 (3 × 4 m) with a solid floor and fresh straw bedding. An overhead CCTV camera recorded the behaviour. The test lasted for 45 minutes after which all pigs were returned to their home pen. The frequency and duration of fights of the focal pigs were observed from video by a single observer, while noting the identity of the opponents, which enabled calculation of whether they fought with unfamiliar pigs, pen-mates or siblings from a different pen more often than expected by chance.

638 *4.2.8 Behavioural observation of the social support test (Publication 4)*

639 An overhead CCTV camera recorded the social support test from above while a sports
640 camera (GoPro) recorded the sound and the view facing the pig's head. The overhead video was
641 used for recording behaviour, and the front-facing camera was used for scoring vocalizations. The
642 behaviour of the focal animal was recorded using the ethogram described in **Table 2**. The initial
643 ethogram also included lying, sitting, escape attempts and urinating (following the ethogram
644 described in Reimert et al., 2014), but these behaviours were removed as they did not occur.
645 Behaviours were scored as frequencies, and the duration of head proximity and snout proximity
646 was scored in seconds. For the non-social behaviours (standing alert and attempting to turn) a
647 distinction was made between the solitary phase and the social phase. The observation started as
648 soon as the door of the weigh crate was closed and ended when the companion was removed.
649 Behaviours were scored using Windows media player. Audio recordings of vocalizations were
650 available for 18 pigs (10 males and 8 females, balanced by treatment) due to a technical error with
651 the camera on some test days. High- and low pitch vocalizations of the focal pigs were coded in
652 Boris V.8.21.8 (Friard and Gamba, 2016). High-pitched vocalizations included screams, squeals
653 and grunt-squeals while low-pitched vocalizations included short and long grunts (Reimert et al.,
654 2014). Each single vocalization was scored as an event and summed by pig to obtain the total
655 amount of vocalizations.

656 To account for the behaviour of the companion, the duration (in seconds) of the companion
657 being in direct proximity (<30 cm) of the weigh-crate was recorded. Additionally, the behaviour
658 of the companion was scored using a 3-point scale: 1) Calm: engaged in exploration, walking, or
659 social contact. Does not show stress-related behaviour (see 2 and 3); 2) Restless: spends time at
660 the exit and may push the exit door with its snout. May show defecation or freezing behaviour; 3)
661 Stressed: showing signs of distress, including escape attempts by climbing the exit door with the
662 front legs or jumping against the door. The videos were observed by a single observer (intra-
663 observer reliability of 0.92), and 20% was scored by another observer to determine inter-observer
664 reliability (score of 0.99).

665

Table 2. Ethogram for behaviour of the focal pig during the social support test. Social behaviours are only scored after the entrance of the companion (social phase). Behaviours were scored as frequencies, and snout proximity along with head proximity were additionally scored as duration.

Behaviour	Description
Standing alert (freezing)	Resting on all four legs without moving off its position for > 3 s. Does not engage in any other behaviour. May include freezing behaviour.
(Attempt to) turn	Moves its head in the direction of the opposite site of the crate, thereby curving the body to change position and exerting pressure on the side of the crate. Includes attempts or full turns.
Head proximity	Has its head <30 cm from the head of the companion, with the heads being in any orientation, except snout proximity.
Snout proximity	Snout of the focal animal is touching or close to touching the snout of the companion
Aggression	Shows agonistic display behaviour or attempts to bite through the crate. Scored for the focal animal and companion separately.
Defecating	Defecates when inside the crate
Tail down	Tail is uncurled and hanging loosely or being held tightly against the body

4.2.9 Saliva sampling and cortisol analysis (Publication 4)

To assess the stress response of the focal pig in the social support test, saliva samples were taken at four time points: just prior to the test (t0), directly after the test (sample taken when the pig was still in the crate) (t4), and at 30 (t30) and 60 minutes (t60) after the test, when they were back in their home pen. Samples were collected using the Salivette® Cortisol synthetic swab with Salivette® Cortisol tube (Sarstedt, Germany). The swab was secured with a plastic zip tie that was always held by the researcher to prevent the pig from swallowing the swab. During the preparation, collection and storage of the samples the handlers wore disposable latex gloves to avoid contamination of the sample. The swab was introduced in the pigs' lower cheek, letting it free to open or close the mouth. The swabs were left in the mouth for 40 seconds. If the animal rejected the swab by spitting it out, then the swab was reintroduced. The swab was then placed in the Salivette® tube and placed in a styrofoam box with ice. Within 3h after collection, samples were transferred to a -80ºC freezer and stored until laboratory processing.

For analysis, the collected saliva samples were thawed on ice and centrifuged for 10 minutes at 2000 × g at +4°C. Next, the saliva was transferred to sterile 2 ml Eppendorf tubes and subjected to a second centrifugation for 20 min at 1500 × g at 4 °C. The supernatant was collected

and used for further analysis. Cortisol concentrations were measured using an enzyme-linked immunosorbent assay (Saliva Cortisol Enzyme Immunoassay Kit, Salimetrics, USA), following the manufacturer's instructions. Each sample was analysed in duplicate. Each plate included six standards with known cortisol concentrations and a blank sample containing no cortisol. To minimize inter-assay variability, all samples from the same individual were analysed on the same microplate. Absorbance was measured at 450 nm using a microplate reader. For each sample, two independent optical density readings were obtained and averaged. The B/Bo ratio was calculated, where B represents the mean optical density of the sample and Bo the mean optical density of the blank sample. Cortisol concentrations (µg/dL) were interpolated from a standard curve fitted using a four-parameter logistic (4PL) regression model suitable for ELISA data. All calculations were performed using R software (R Core Team, 2023) (version 4.2.3).

5. Statistical analysis

All statistical analyses described in this thesis were performed in the statistical program R (Publication 1-2, 4: R version 4.3.2; Publication 3: R version 4.1.3).

5.1 Mixed Modelling (Publication 1)

A moderate correlation was found between initiating and receiving snout contact ($r = 0.38$, $p < 0.001$), snout proximity ($r = 0.31$, $p < 0.001$), and aggressive behaviour ($r = 0.32$, $p < 0.001$). This suggests that individuals engaging in these behaviours are also likely to be recipients, indicating possible reciprocity. Given this correlation, only data from the initiator was included for analysing social behaviours, while both initiators and recipients were considered when examining associations with ADWG. Additionally, a correlation analysis was conducted between Modified David's Score (MDS) and ADWG, as well as between aggressive behaviour, snout proximity, and snout contact. The analysis was performed using the "cor.test" function in R. Since not all animals had the same number of observations, behaviour frequencies were averaged per 15-minute session by dividing the total occurrences by the number of sessions per animal.

Three linear mixed models were developed in R (version 4.3.2) using the lme4 package lmerTest (version 3.1-3) (Kuznetsova et al. 2017). In the first model, the response variable was the

frequency of snout contact or frequency of snout proximity per session, while predictor variables included social stability, housing conditions, socialization, sex, and MDS. Pig ID was nested within group and batch as a random effect. The second model considered ADWG as the response variable (analysed separately for initiators and recipients), with predictor variables including snout contact, snout proximity, aggression, housing conditions, socialization, and sex, while pig ID nested within group and batch was used as a random effect. In model 3, the frequency of snout proximity and snout contact towards related (littermates) and unrelated conspecifics (non-littermates) was analysed separately in a mixed model. The response variable was the frequency of snout proximity or snout contact (two separate analyses). The predictor variables were housing condition, sex, socialization, and social stability, with as random variables pig ID and group nested within batch. In model 3, the frequency of snout proximity and contact towards related (littermates) and unrelated conspecifics (non-littermates) was analysed separately in a mixed model with snout proximity and contact as response variables, and as predictor variables housing condition, sex, socialisation, and social stability.

The best-fitting model was chosen based on the lowest AIC value following a backward selection process, which ensured that only the most relevant variables were retained. Model diagnostics were performed on the final model to assess normality, homogeneity of residuals, and collinearity among predictor variables. The Shapiro-Wilk test confirmed that residuals were normally distributed, while homogeneity was verified through visual inspection of residual plots against fitted values using the sjPlot package (Lüdecke, 2024). Cook's distances were calculated and plotted to identify influential data points, with no values exceeding 1 across all models. Multicollinearity was assessed using the variance inflation factor (VIF) from the "car" package (Fox and Weisberg, 2018), with results indicating no significant collinearity (VIF < 2). Post-hoc analyses were conducted using the "emmeans" package (Russell, 2020) to determine least square means (LSmeans) with standard errors (SE). P-values were estimated using the model summary function and were considered statistically significant at ≤ 0.05. Figures were made using the "ggplot2" package (version 3.5.1) (Wickham, 2016).

5.2 Network measures at Group level and Individual level (Publication 2)

5.2.1 Network analysis

Social network analysis helps to understand social associations at the individual and group level (Krause et al., 2007; Wey et al., 2008). In network theory (Wey et al., 2008), a social group with more than two members (also called actors or nodes) is connected via social relationships or interactions. These connections (referred to as edges) can be one-directional (unilateral) or bi-directional (reciprocal). The frequency of interactions provides weight to the relationships. Various individual and group network measures can be utilised to understand the variation in social associations (Pasquaretta et al., 2014; Sosa et al., 2021). Based on previous studies (Makagon et al., 2012; Pasquaretta et al., 2014), we chose clustering coefficient, average local efficiency, degree centralisation, modularity, and assortativity as the group-level network measures (n=15 groups) (**Table 3**). These measures describe whether (i) the network is centralised around one individual, (ii) the flow of social information occurs quickly through the group, (iii) the network has a high tendency, among the nodes, to form clusters indicating a high level of local interconnectedness, (iv) the network divides into communities with nodes in the same community densely connected, whereas sparse connections exist between different communities and (v) whether individuals direct snout contact behaviour towards individuals with similar traits.

At the individual level, we included measures of degree centrality, eigenvector centrality (Sosa et al., 2021), R-index (Liao et al., 2018) and node level clustering coefficient. These measures describe whether (i) the number of social partners and the frequency of association across the period of group integration changes during social integration, (ii) individuals' social positions change over time, (iii) the degree to which nodes in a network tend to cluster together forming a clique (a network of fully connected individuals), and (iv) individuals are more active in performing the role of initiator or recipient in social interactions.

Behavioural data from 15 groups were included for analyzing five group-level network measures (**Table 3**) using the library "igraph" in R (Csárdi et al., 2025). Out of 15 groups, two groups consisted of seven individuals (due to pigs being removed for health reasons), and the remaining groups had eight individuals.

Table 3. Description of the group- and individual-level social network properties.

Network measure	Purpose	Value range
Group level		
Degree centralization	Measures the extent to which snout contact is concentrated on a single or few individuals.	0 (decentralized network) to 1(centralized network)
Average local efficiency (out-degree)	Indicates the spread of a behaviour as indicated by the average number of social partners an individual interacted with as the initiator.	0 to 1 (efficient transmission of behaviour)
Clustering coefficient	Measures the cohesion between individuals in a group, as indicated by the proportion of fully connected triads in the group.	0 (no cohesion) to 1 (cohesion)
Modularity	Measures the fragmentation of a group.	0 (random relationships) to 1 (strong hierarchical clustering)
Assortativity	Determines the tendency of nodes to connect to other nodes that are similar in some attributes.	-1 (nodes tend to connect to nodes with different attributes) to 1 (same attributes between nodes)
Individual level		
R-index (social role)	Measures individuals' inclination towards acting as the initiator. $RI_i = wo_i/(wi_i + wo_i)$, where RI_i is the R-index of individual i, wo_i is the weighted outdegree, and wi_i is the weighted indegree. In- and out-degree indicates the number of social partners an individual received contact from (in-degree) or initiated contact with (out-degree), weighted by frequency.	>0.5: an individual undertakes the role of initiator
Degree centrality: unweighted out-degree	Unweighted centrality: as above (for group-level),	0 (no social partner) to 6 or 7 (max. number of social partners per individual, in this study)
Degree centrality: weighted out-degree	Weighted centrality: to measure the variation in the amount of initiated behaviour as the group integrates; weighted by frequency of contacts initiated towards social partners.	0 (infrequent contact) to max frequency of contact
Eigenvector centrality (social position)	Measures the social position of a node based on the connections of the node to whom the focal node is connected in a social group.	0 to 1; the higher the more the focal individual connected to well-connected individuals.
Node clustering coefficient	Measures a node's neighbours' inclination to form a complete clique (a fully connected subgraph).	0 (no cohesion between neighbours of a node) to 1 (max. cohesion)

Normalised values adjusted for group size were used whenever the network measures accommodated normalisation. Behavioural data were collected using a combination of live observation and video decoding. To assess whether the social networks differed based on the inclusion of video data, networks for live observation only and networks for live+video data were compared using Hamming distance. Hamming distances (a value from 0–1; whereby 0 denotes identical networks) for all three batches showed that the network structures remained mostly

similar (batch 1, range: 0–0.14; batch 2, range: 0–0.01; batch 3, range: 0–0.02). Since Hamming distance only considers binary values (presence or absence of a connection between individuals), a correlation of degree centrality was performed between the live observation and live+video observation networks to confirm that the networks created from the inclusion of video observation data were not aberrant. A negligible correlation was observed in two groups (-0.08 – 0.07), a moderate correlation in another two groups (0.31 – 0.51), and a high correlation in 11 groups (0.79-0.98), suggesting that inclusion of video observations did not alter the structure of the networks compared to networks based on live observations. It should be noted that a perfect correlation is not expected since the addition of the video data increased the sample size which likely affected the network structure. Hence, live and video data were combined and the differences in the network metrics at group level across phases of integration were tested using a paired Wilcoxon signed rank test.

5.2.2 Model selection for individual level network measures

Measures from social network analysis, calculated from the igraph library and, node clustering coefficient using the "DirectedClustering" package (version 0.1.1) (Clemente and Grassi, 2018), were built into mixed models as response variables to measure the effect of different predictor variables such as early-life socialisation treatment (socialised or non-socialised), housing condition (ENR or CON), sex (male or female), and social stability (low, medium, high), on the network measures. Batch and individual ID (nested within the group), were included as random factors. Firstly, we performed a generalised mixed model with binomial distribution using the "glmer" function in the "lme4" package (Bates et al., 2015) (version 1.1-35.1). Individual-level social network measures of degree centrality (unweighted and weighted out-degree centrality) and R-index (for initiation of the behaviour) were response variables in the three separate models. In the model with the unweighted degree centrality as the response variable, the specific binomial structure was defined as the number of unique social partners based on the theoretical maximum possible number of social partners, and in the model with weighted degree centrality as the response variable, the structure was defined as the frequency of social associations for each social partner based on the maximum number of social associations. Similarly, the individuals' social role (R-index, whereby ratios ≥0.5 indicates the animal as an initiator) as response variable was included in another binomial mixed model.

Another model with a beta distribution was built for the proportional response variable eigenvector centrality (where higher values denote that individuals occupy a more central position in the group interacting with well-connected partners). Since eigenvector centrality values are in the range from zero to 1, the value of zero was changed to “0.0001” and “1” into “0.9999” to accommodate the mixed model using glmmTMB (Brooks et al., 2017) (version 1.1.9) in R. Similarly, individuals' local clustering coefficient based on weights (frequency of association) was modelled using a beta distribution. Post-hoc tests were performed using the “emmeans” package (version:1.8.9) (Lenth, 2024).

5.3 Tenor and social preferences (Publication 2)

The nature of associations was analysed using the Tenor index as proposed by Silk et al. (2013). The tenor index shows whether the behaviours are mostly affiliative (value close to 1) or mostly hostile (value close to 0). The tenor was calculated, for each social stability phase, as the frequency of affiliative behaviour per observation period divided by the frequency of all affiliative and agonistic behaviour summed (following Fischer et al., 2017).

Normality and variance of the association data were tested using Shapiro-Wilk test and Levene’s test. A repeated measures Anova analysis was performed, followed by a post-hoc paired t-test with Bonferroni correction to test the differences between the social stability phases for snout contact behaviour. Variability in the association pattern was tested via Monte Carlo permutation. The strength of social associations among pairs of individuals was based on the frequency of snout contact and analysed via a Monte Carlo permutation test. Association matrices based on snout contact were constructed for each group (15 groups) across 3 social stability phases, resulting in 45 association matrices. The permutation test was performed using the library "ade4" (Dray and Dufour, 2007) (version 1.7-22) and “vegan” (Oksanen et al., 2024) (version 2.6-8) to analyse if snout contact was directed towards preferred social partners significantly more than by chance. When the observed coefficient of variation (CV) was greater than the random matrix in more than 95% of the permutations ($p < 0.05$), the variability in the preferential association matrix was considered non-random and significant (Patriquin et al., 2010; Manly, 2018). A total of 1,000 random permutations were generated from observed association matrices, by allowing the total

number of individuals and the number of associations from the observed matrix to be the same (Bejder et al., 1998; Whitehead et al., 2005) and the p-value based on permutation was calculated.

Additionally, the influence of litter origin and early-life socialization was calculated using the Mantel permutation test on the half-weight index (HWI; explained below) (Cairns and Schwager, 1987). The HWI was calculated to quantify the strength of the associations between individuals across time (low-medium and medium-high social stability), and a Mantel test was performed to estimate how the association was affected by traits of the individuals such as relatedness and early-life socialization. The Mantel test with 1,000 permutations was performed to examine the association depending on individuals' litter origin, using the "dist" function from the "vegan" package (Oksanen et al., 2024**)**. The Mantel test measures whether the pattern of differences (or similarities) between pairs of items in one matrix is correlated with the pattern in another matrix (Legendre et al., 2015). The HWI was calculated as, $X/ (X+Y_{ab}+0.5(Y_a+Y_b))$, where X is the frequency in which "individual a" and "individual b" were reciprocally interacting, Y_{ab} is number of times both individual "a" and "b" are located separately in different groups, Y_a is the number of times "individual a" initiated interaction with "individual b" but not "individual b" with "individual a" (i.e. a's interaction was not reciprocated), and Y_b is the number of times "individual b" initiated interaction with "individual a" but not "individual a" with "individual b". As the observations were performed in a closed system (no change in group composition after regrouping), individuals could not be located separately in different groups. Hence, the term "Y_{ab}" in the HWI equals zero, and the HWI calculation changes to, $X/(X+0.5(Y_a+Y_b))$, like the modification performed in previous studies (Lusseau et al., 2003). After considering the HWI, a dissimilarity matrix based on two social stability phase comparisons (e.g. low-mid) for each dyad, including a distance matrix based on the grouping variable (litter origin, socialisation), was constructed.

5.4 Mixed modelling (Publication 3)

Data analysis was conducted using two distinct datasets. The first dataset contained repeated measurements for individuals across three testing days to evaluate consistency of leadership (n = 366 individuals from 32 groups). The second dataset focused on individuals with a single binary classification (leader/follower) from the initial test where a clear leader was

identified (n = 289 individuals from 26 groups). Due to the absence of a distinct leader, six groups were omitted from the second dataset. Statistical significance was determined at p-values ≤ 0.05.

From the first dataset, the consistency of leadership (binary variable) was examined using the "rptR" package (Stoffel et al., 2017) with 1000 bootstrap iterations and a binary data structure. The model incorporated body weight at weaning (kg, measured at week 4), sex (male/female), and coping response (number of struggles) as fixed effects, while pig ID and group ID were included as random effects. Furthermore, another model was performed with the latency to touch the human as the response variable, with the body weight at weaning, sex (male/female), and the interaction between test day and leadership outcome along with their main effect as fixed effects, while pig ID and group ID were included as random effects.

The association between leadership, backtest outcomes, and body weight was explored using the second dataset. In this analysis, leadership (yes/no) served as the response variable in a generalized linear mixed model, implemented via the "lme4" package (Bates et al., 2015), utilizing a logit link function for binomial data while predictor variables included weaning body weight, sex, and coping response. Initially, both the number of struggles and vocalizations were considered; however, due to their correlation (Spearman correlation: $r = 0.75$; $p < 0.001$), only the number of struggles was retained for optimal model fit, based on the lowest AIC and BIC values. Random effects included batch (cohort) and group within batch. To assess differences between levels of the categorical variable (sex), post-hoc pairwise comparisons were conducted using the "emmeans" package (Lenth, 2021) in R.

5.5 Measures of social support (Publication 4)

5.5.1 Behavioural analysis (Mixed modelling)

Data were analysed using linear mixed models and generalised linear mixed models in R version (4.3.2) (R Core Team, 2023). The “lme4” package (Bates et al., 2015) was used (unless stated otherwise) to perform linear mixed models with a Gaussian distribution. The “lmerTest” package (version 3.1-3) (Kuznetsova et al., 2017) was used to perform generalised linear mixed models with Poisson distribution, and negative binomial distribution. Stepwise backward

894 regression was performed on the full models to select the best fitting model based on the lowest
895 AIC. Models were assessed for diagnostics including uniformity in residuals, overdispersion, and
896 zero-inflation. The residuals of the model were assessed from Shapiro-Wilk statistics.
897 Homoscedasticity was assessed via visual inspection of residual plots against fitted values. Cook
898 distances were calculated and plotted to identify influential data points (threshold set at 1).
899 Multicollinearity detection was performed using the variance inflation factor, using the "car"
900 package (Fox and Weisberg, 2018). The variance inflation factor did not indicate strong
901 multicollinearity (<2) in any of the models. Post-hoc comparisons were conducted using the
902 "emmeans" package (Russell, 2020) to obtain the least square means (LSmeans) with standard
903 errors (SE). Values were considered significant at $p<0.05$. All data figures were made in R using
904 the "ggsave" function from the "ggplot2" package (version 3.5.1) (Wickham, 2016).

905 The behaviours aggression, defecation, and tail posture showed too little variation to enable
906 analysis and were therefore presented descriptively. However, a binomial test was performed to
907 confirm if these behaviours were chance occurrences or not. The frequency of standing alert and
908 turning behaviour from the social phase (3 min.) was scaled to one minute to match the duration
909 of the solitary phase and was thereafter compared using the Wilcoxon signed-rank test. The
910 Shapiro-Wilk test was used to determine the normality of the distribution of standing alert and
911 turning behaviour.

912 The duration of snout proximity was analysed as a response variable in a linear mixed
913 model, using the "nlme" package (Pinheiro et al., 2023) (version 3.1-164). The predictor variables
914 were social treatment (strong / weak relationship), housing condition (barren / enriched), and sex
915 of the companion (male / female), with the frequency of turning and standing alert in the social
916 phase as covariates. Group, nested within batch, was included as a random effect. Snout proximity
917 shown by the focal pig correlated moderately with spatial proximity of the companion ($r = 0.489$,
918 $p = 0.005$), and therefore, proximity from the companion was excluded from the model to avoid
919 multicollinearity. The best-fitting model included only the social treatment.

920 The duration of spatial proximity of the companion was analysed as a response variable in
921 a separate linear mixed model to examine whether the companion was influenced by the focal pig.
922 The predictor variables were the social treatment, sex of the companion, and the sum of stress-

related behaviours of the focal pig (sum of tail down, aggression, turning, standing alert, and defecation). Group, nested within batch, was included as a random effect.

The frequencies of head proximity, snout proximity, turning and standing alert were analysed as response variables in generalised mixed models with Poisson distribution, as the response variable was count data (without zero-inflated frequency). The predictor variables were social treatment, housing condition, and sex of the companion. Turning and standing alert were added as covariates in the models of head and snout proximity. Group nested within batch was included as a random effect. The best fitting model for head proximity included the social treatment, sex of the companion, and standing alert. The best fitting model for snout proximity included the social treatment, housing condition, and turning behaviour. For turning and standing alert the full models were retained.

5.5.2 Analysis of vocalizations

The frequency of vocalizations was divided into the solitary phase (1 min.) and the social phase (3 min.), whereby the vocalizations from the solitary phase were used to ascertain whether differences between the treatment groups were not already existent before the treatment started. Low pitch vocalizations in the solitary phase and social phase were analysed as response variables in generalised mixed models with Poisson distribution. For the analysis of vocalizations only, we performed a forward step selection from the null model to select the best fitting model, and model diagnostics were performed using the "DHARMa" package (version 0.4.6; Hartig, 2022). High pitch vocalizations were analysed as response variables in a generalised mixed model with negative binomial distribution to account for heteroscedasticity. The predictor variables for both the low pitch and high pitch variables were the social treatment, housing conditions, sex of the companion, the focal pigs' body weight (with quadratic term included only for low pitch model), as well as the interaction between treatment and body weight (as body weight influences vocalizations in pigs: Garcia et al., 2016). Group ID was included as a random effect. The quadratic term for body weight during low pitch vocalizations was included as body weight did not show a linear association with low pitch vocalizations, which was also confirmed by examining the residuals. The full models were retained as best model fit.

951 *5.5.3 Analysis of cortisol concentrations*

952 The cortisol values for t0, t4, t30, and t60 were subtracted from each other to obtain the
953 difference between each two consecutive time points. The values were then divided by the initial
954 cortisol value at the time point to obtain a proportional change in cortisol values. This resulted in
955 three values per pig, which were analysed as repeated values in a linear mixed model to test if the
956 changes in cortisol concentration were influenced by any of the predictors. Both the original
957 cortisol values (t0, t4, t30, and t60) and the proportional change (t0-t4, t4-t30, t30-t60) were
958 analysed in a linear mixed model with social treatment, housing condition, sampling period and
959 daytime (am / pm) as predictor variables and body weight of the focal pig as covariate. Pig ID (to
960 account for repeated measures) and group ID were included as random factors.

961 *5.5.4 Analysis of social differentiation*

962 Dyadic fights were classified into three groups: fights between unfamiliar pigs, between
963 siblings who were kept together as pen mates, and between siblings that were separated (not pen-
964 mates). Since the group composition at regrouping varied slightly between batches, we calculated
965 for each individual the probability of encountering pigs from each familiarity category and
966 averaged the expected proportion per batch. A one-sample proportion test, using the "prop.test" in
967 R for an expected proportion (here based on mean encounter), was tested under the null hypothesis
968 using a chi-squared statistic to test the differences in the number of fights for the categories. Fight
969 duration was analysed as a response variable in a generalised mixed model with a Gamma
970 distribution (as the duration was not uniformly distributed). The predictor variables were the
971 familiarity category (unfamiliar siblings kept together and siblings separated), same sex dyad (yes
972 / no), sex of the initiator (m / f) and the difference in body weight between opponents, with group
973 as a random effect.

974

6. Results

6.1 Potential presence of behavioural trade-off (Publication 1)

6.1.1 Hypothesis 1: Individuals choose non-tactile behaviour when risks are high

We predicted that pigs would show snout proximity when costs (in terms of aggression) are high and show more snout contact when risks are low. On average, pigs showed 0.46±0.33 (mean ± SD) snout proximity interactions per pig per 15 min, and 0.82 ± 0.48 snout contact interactions per pig per 15 min. The frequency of snout proximity differed between the social stability phases (P <0.001, model 1 in publication 1), with the highest frequency during low social stability, while there was no significant difference between the medium and high stability phase (**Figure 4**). The frequency of snout contact was lower during the medium stability phase (Low – Mid: 0.10 ± 0.039, P = 0.02; Mid – High: -0.13 ± 0.040, P = 0.002, model 1, in publication 1) while being numerically but not significantly higher in the phase of high social stability. There was a positive correlation between snout proximity and snout contact in all phases of social stability (Low: r = 0.75, P <0.001; Medium: r = 0.52, P <0.001; High: r = 0.61, P <0.001).

Aggressive behaviour was positively correlated with snout proximity (r_{range}: 0.34 – 0.65; P <0.001) and snout contact (r_{range}: 0.4 – 0.66; P <0.001) across the phases of social stability. The Modified David score (MDS) did not relate to the expression of snout proximity (P = 0.42; model 1, publication 1) but did relate to the expression of snout contact (b = 0.006 ± 0.002; P = 0.03; model 1, in publication 1) indicating that pigs with higher dominance value initiated more snout contact. There was no correlation between dominance (MDS) and body weight gain (ADWG; r = 0.01; P = 0.89). Males expressed more snout proximity than females (males: 0.54 ± 0.126; females: 0.46 ± 0.126 times / 15 min; P = 0.002) but did not differ from females in the frequency of snout contact (P = 0.48). Pigs in the more enriched housing conditions showed less frequent snout proximity (ENR: 0.46 ± 0.114 times / 15 min *vs.* CON: 0.52 ± 0.114 times / 15 min; P = 0.02, model 1, in publication 1) and snout contact (ENR: 0.81 ± 0.184 times / 15 min *vs.* CON: 0.94 ± 0.184 times / 15 min; P = 0.01, model 1, in publication 1). Pre-weaning socialization did not influence the snout proximity (P = 0.80) or contact (P = 0.65).

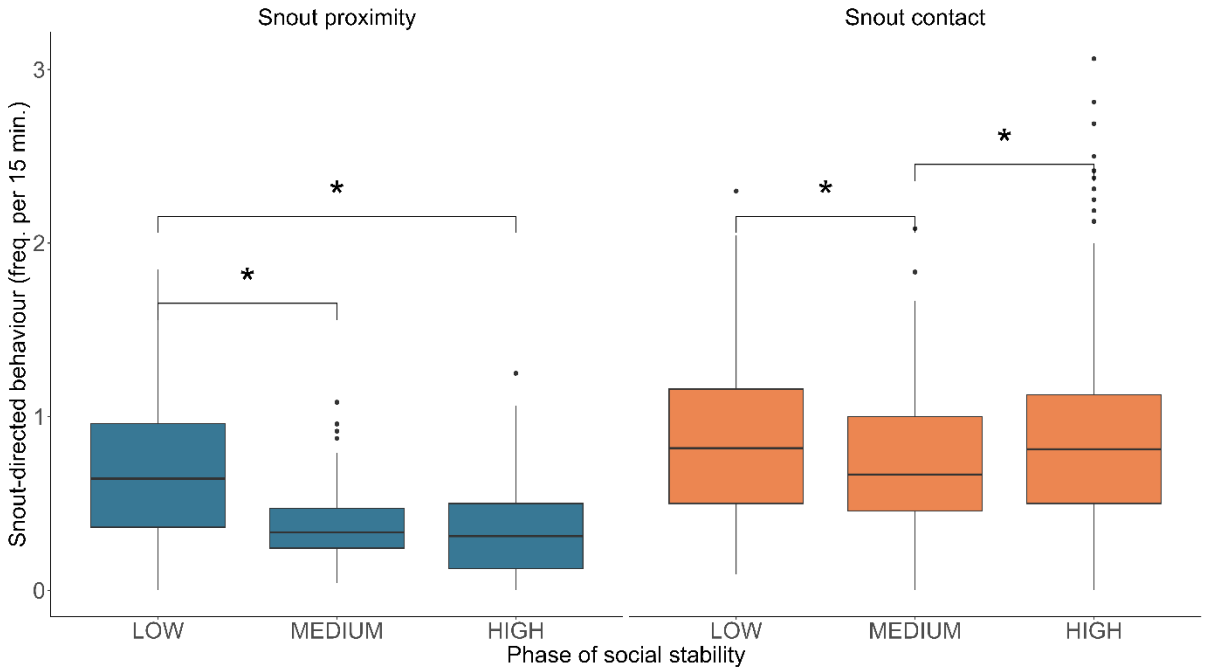


Figure 4. Average frequency (per pig per 15 minutes of observation) of snout proximity (blue) and snout contact (orange) by phase of social stability. The asterisk indicates significant differences (P <0.05) between the phases.

6.1.2 Hypothesis 2: Individuals derive benefits from tactile contact

Pigs that initiated or received a greater frequency of snout proximity had a lower average daily weight gain (ADWG) than those who did so less (initiator: b = -0.65 ± 0.056 kg/day; P = <0.001; recipient: b = -0.62 ± 0.060 kg/day; P = <0.001; model 2 in publication 2) (**Figure 5**). In line with our hypothesis, frequent initiators and recipients of snout contact had a greater ADWG than those who initiated or received less snout contact (initiator: b = 0.20 ± 0.041 kg/day; P = <0.001; recipient: b = 0.18 ± 0.046 kg/day; P = <0.001; model 2; **Figure 5**). Pigs that received more aggressive behaviour had a lower ADWG (b = -0.11 ± 0.030 kg/day; P = <0.001; model 2, in publication 1) whereas for the initiator aggression was not significantly associated with ADWG (P = 0.43).

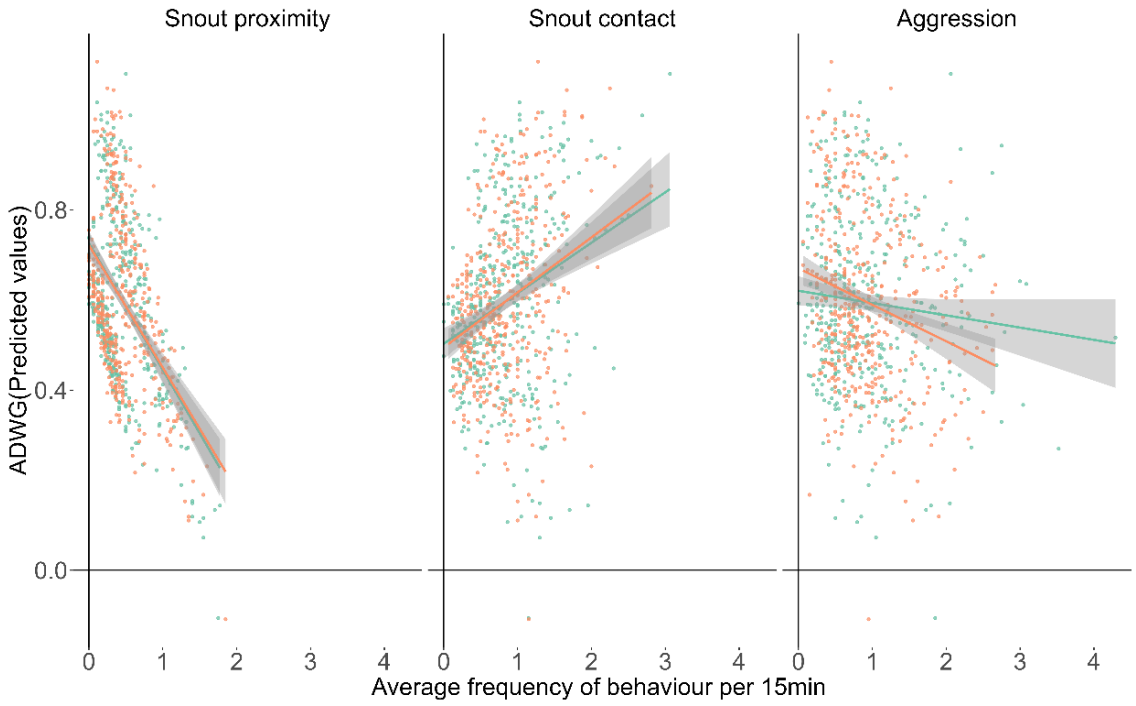


Figure 5. Relationship between the average daily weight gain (ADWG, in kg / d) and behavioural expression of snout proximity, snout contact and aggressive behaviour for initiators (teal) and recipients (orange) of the behaviour. The x-axis shows the average frequency of behaviour per 15 minutes. Predicted values refer to the fitted response value from the model.

6.1.3 Factors affecting snout proximity and contact

Unrelated conspecifics showed more snout proximity towards each other compared to related conspecifics (non-littermates: 0.31 ± 0.013, *vs.* littermates: 0.24 ± 0.077 per pig per 15 minutes, P <0.0001) and more snout contact (non-littermates: 0.31 ± 0.077 *vs.* littermates: 0.24 ± 0.077, P <0.0001). In the phase of low social stability, related pigs (littermates) showed more frequent snout proximity towards each other than in the later phases (P <0.001, model 3; **Figure 6**).

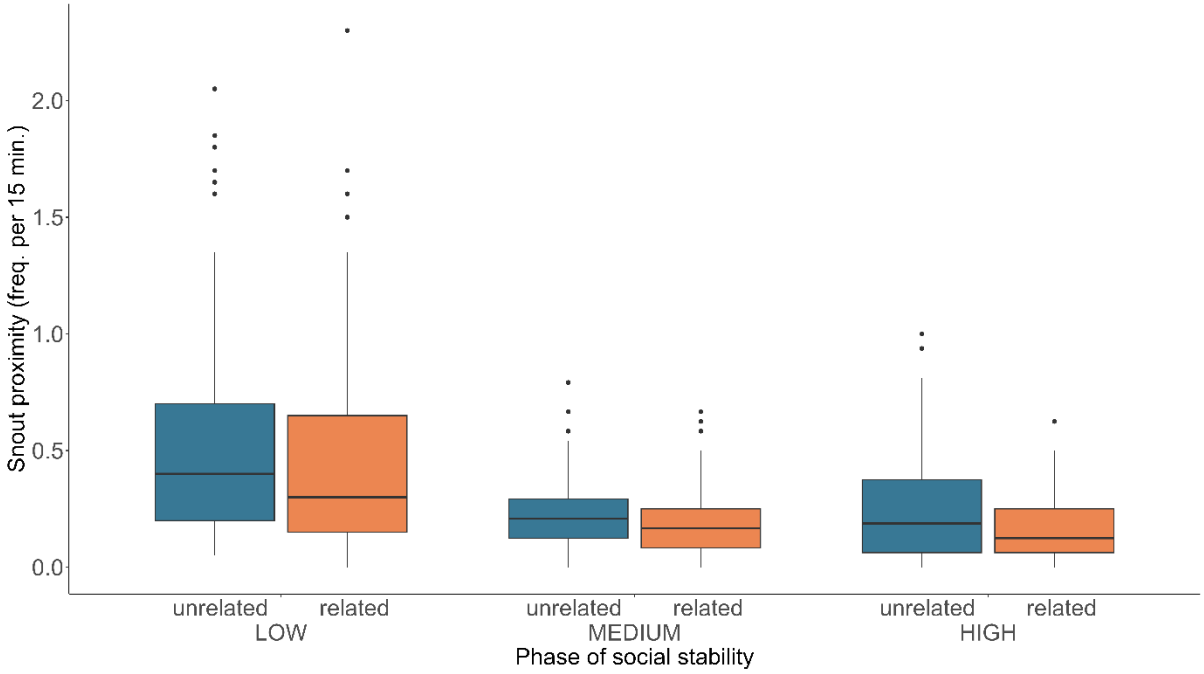


Figure 6. Frequency of snout proximity (per 15 min.) directed towards unrelated pigs (non-littermates; blue) and related pigs (littermates; orange) during the phases of low, medium and high social stability.

6.2 Social network of snout contact behaviour (Publication 2)

6.2.1 Temporal variation in group-level network properties

Across 15 groups (118 pigs), a total of 7,521 snout contacts were recorded based on 56.5 hours of observation (mean interactions per group 501.4; SE = 4.18). Overall, there was little variation in the network measures across the integration phases. However, differences were found in certain network measures at the group level between the low and medium social stability phase. Specifically, average local efficiency increased in the medium stability phase (paired Wilcoxon signed-rank test, V = 17, n = 15, p = 0.01) and degree centralisation differed between the low and high social stability phase, whereby degree centralisation increased in the high stability phase (V = 94, n = 15, p = 0.01), indicating that behaviour became increasingly performed by a small number of individuals. The network measures indicate an absence of a clear community structure (as

indicated by modularity) and show high connectivity between the neighbours of nodes (as indicated by the clustering coefficient). Additionally, snout contact appeared to spread only moderately from one node to others (via dyadic efficiency), implying that when an individual engaged in snout contact, this did not encourage others to do the same, and thus, not all individuals engaged equally in snout contact. The network based on snout contact was relatively decentralised (as shown by degree centralisation), indicating that behaviour was not disproportionately performed or received by a small number of individuals. Furthermore, assortativity values indicated that nodes tended to connect with dissimilar individuals (thus showing heterophily) in terms of socialisation treatment and litter origin, indicating that socialised pigs associated more with non-socialised ones (and vice versa) ($V = 28$, $n = 8$, $p = 0.02$) and that individuals from different litters engaged more in snout contact with each other than with litter mates ($V = 28$, $n = 15$, $p = 0.02$).

6.2.2 Temporal variation in individual-level network properties

The number of social partners through snout contact decreased as group integration progressed (measured by unweighted degree centrality) (**Table 4**). While there was no significant difference in this likelihood between the medium and high social stability phases, a difference was observed between the low and medium phase, as well as between the low and high social stability phases for unweighted degree centrality. The frequency of associations, measured by weighted degree centrality which reflects the strength of social ties, declined over time. In the high social stability phase, individuals exhibited less frequent snout contact as observed in the weighted social network (**Table 4**). Taken together with the reduction in unweighted degree centrality over time, this suggests a shift from broad social exploration with many partners, to more focused, repeated interactions with fewer social partners. The eigenvector centrality remained high throughout the observations, resulting in no significant differences between the phases (**Table 4**). Additionally, individuals' likelihood of connecting with other individuals, based on the node clustering coefficient, was higher during the low than the high social stability phase whereas a tendency ($p = 0.06$) for a higher likelihood of nodal clustering was observed in the low as compared to medium stability phase.

Table 4. Network metrics (model-estimated probabilities) from individual-level networks and Odds Ratio (OR) from the best fitting model, based on 118 pigs across 15 groups. Values are emmeans with standard error (SE) based on the frequency of snout contact during low, medium and high social stability.

	Means ± SE			Post-hoc OR		
Network measure	**Low**	**Medium**	**High**	**Low-Mid**	**Low-High**	**Mid-High**
Unweighted degree centrality (out-degree)	0.91 ± 0.044	0.86 ± 0.064	0.84 ± 0.070	1.64*	1.84*	1.12
Weighted degree centrality (out-degree)	0.64 ± 0.020	0.66 ± 0.020	0.58±0.021	0.91	1.2*	1.4*
Eigenvector centrality	0.74 ± 0.022	0.71 ±0.023	0.71 ± 0.023	1.13	1.14	1.01
Node clustering coefficient	0.82 ± 0.061	0.76± 0.074	0.71± 0.085	1.40	1.86*	1.34

6.2.3 Factors affecting individual-level network structure and individuals' social roles

Males were nearly two times more likely to assume the social role of initiator compared to females (OR 1.92, $p = 0.007$, CI [1.188-3.116]). However, females were 1.5 times more likely to occupy more central social positions, reflected by a higher eigenvector centrality (OR 1.5, $p = 0.007$, CI [1.11- 2.02]). Pigs housed in less-enriched environments were more likely to form a greater number of social relationships than pigs in the enriched housing condition (non-weighted out-degree OR 1.79, $p = 0.004$, CI [1.19 - 2.67]). Additionally, individuals in less-enriched conditions were more likely to form clusters within the network (clustering coefficient OR 1.98, $p = 0.031$, CI [1.06 - 3.69]). However, the housing conditions did not influence pigs' eigenvector centrality within the network. Similarly, early life socialisation did not significantly predict the number of social partners, the eigenvector or the clustering coefficient.

6.2.4 Tenor and social preferences

The nature of social relationships, measured using the tenor, indicated that interactions were predominantly affiliative across all three phases (low social stability: 0.59 ± 0.018, medium: 0.52 ± 0.019, and high: 0.61 ± 0.024). The tenor differed between the medium and high social stability phase ($p = 0.02$) and tended to differ between the low and medium social stability phase ($p = 0.06$) (**Figure 7**). The Monte Carlo simulation did not reveal significant preferred associations between social partners based on snout contact, across any phase of social stability. Although the observed coefficients of variation (CVs) for snout contact were often higher than the mean random CVs, none of the observed CVs exceeded the 97.5th percentile of the random distribution. This indicates that the observed patterns were not significantly different from what would be expected by chance. Specifically, in none of the groups or phases did the observed CV fall outside the 95% confidence interval of the randomised CVs, as reflected by p-values all above 0.05. While 10 groups showed observed CVs greater than the random CVs across all three phases, and 5 groups showed this pattern in one or two phases, these differences were not statistically significant. Therefore, the results suggest that there was no evidence for consistent or structured preferential associations based on snout contact during any of the phases. Further, there was no evidence of temporal stability (based on the Half Weight Index permuted 1000 times) across the phases of social stability due to traits such as relatedness (litter origin: $n = 15$ groups, Mantel test $p > 0.05$) and early life socialisation ($n = 8$ groups, Mantel test $p > 0.05$).

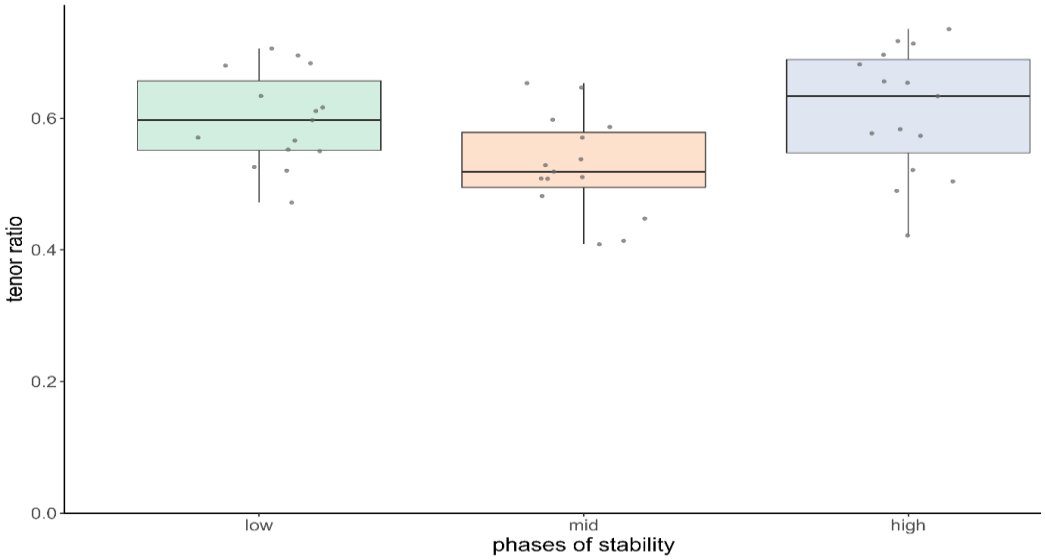


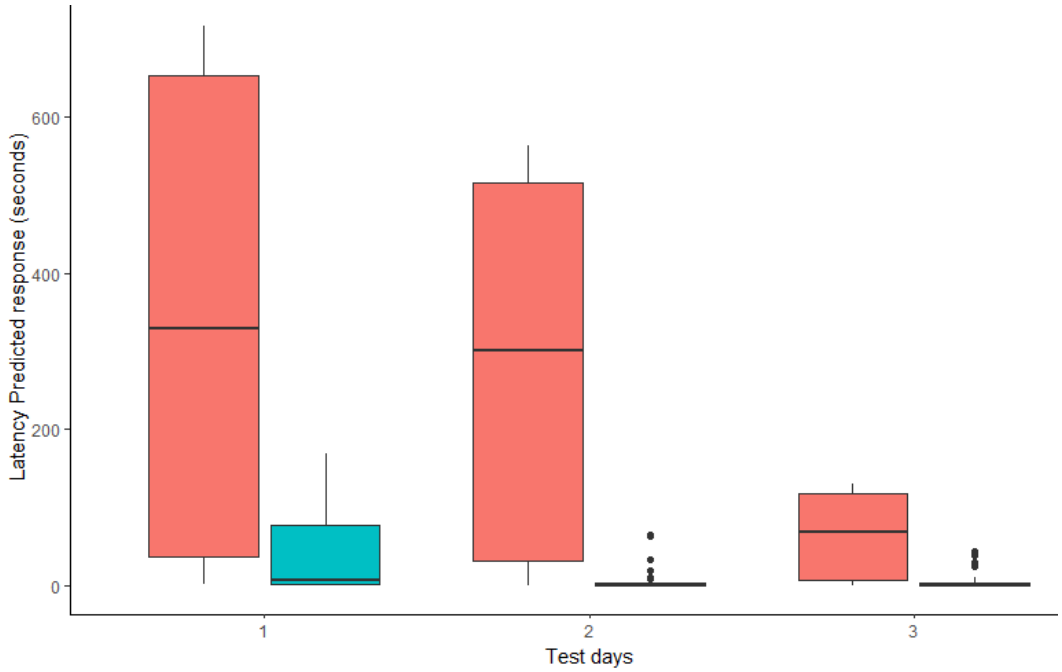
Figure 7. A boxplot showing mean values for a tenor ratio representing the affiliative nature of association (value close to 1) or hostile association (value close to 0) across the phase of integration**.** Based on a post-hoc paired t-test with Bonferroni correction, significant differences between mid-high ($p = 0.02$) and a tendency between low-mid towards affiliative association ($p = 0.06$) was observed.

6.3 Leadership in a novel task (Publication 3)

6.3.1 Repeatability of leadership

On the first test day, 22 out of 32 groups showed no clear distinction between leaders and followers as 43 % of the pigs did not touch the human. Leadership at the individual level was repeatable but only marginally ($R = 0.095$; $p < 0.001$), which was similar at the group level ($R = 0.202$; $p < 0.001$). Across three days of tests, 18 pigs from 11 groups attained a consistent leadership position. Six groups had a single consistent leader while five groups had multiple consistent leaders that were equally fast in the test. The remaining groups did not have pigs that attained a consistent leadership position. Post-hoc analysis showed that the latency to touch the human decreased across test days within followers and leaders (**Figure 8**). For followers, all pairwise comparisons between days were significant ($p <0.001$). The latency to touch the human

1131 significantly differed, in the post-hoc pairwise comparison within leaders, between day 1 and 2 (p
1132 = 0.032) and day 1 and 3 (p = 0.008), but not between day 2 and 3 (p = 0.817). The followers were
1133 also quicker across test days in completing the task right after the leader (day 1: 39.3 ± 6.40, range:
1134 1– 487 s; day 2: 27.9 ± 5.93, range: 1– 548 s; day 3: 16.2 ± 3.30, range 1– 520 s).



1135

1136 **Figure 8.** Boxplot of the predicted latency (in seconds) of leaders (green) and followers (orange)
1137 to touch the human in the Human Approach Test, across the three test days.

1138

1139 *6.3.2 Predictors of leadership*

1140 The number of struggles, as an indicator of coping style, was not a significant predictor of
1141 leadership (b = −0.361 ± 0.21; z = −1.7; p = 0.08). Similarly, body weight at weaning did not
1142 predict leadership (p = 0.91). Body weight did not differ significantly between males and females
1143 (p = 0.25). However, females were more often leaders than males, as shown by a negative
1144 association between males and leadership (GLMM: estimate = −1.41; z-value = −2.91, n = 289; p
1145 = 0.003). From the 26 leaders (classified as leader based on touching the human first on day 1),
1146 only six were male. Post-hoc analysis showed that the probability for females to be classified as

leader was 0.137 ± 0.029 while for males this was 0.037 ± 0.015, resulting in 4.13 greater odds for females to attain a leadership position.

6.4 Social support (Publication 4)

6.4.1 Behaviour of the focal individual

All but one pig showed at least one of the stress-related behaviours of trying to turn around in the crate or standing alert (freezing). Attempts to turn around in the crate occurred more frequently before the entry of the companion (mean ± SD: 2.3 ± 2.22) than when the companion was present (0.7 ± 0.55) (Wilcoxon signed-rank test: $z = -3.34$, $n = 26$; $p < 0.001$), showing that the companion's presence did influence the behaviour. Standing alert did not differ significantly between the solitary and social phases ($z = -1.78$, $n = 27$; $p = 0.08$). Aggression, tail down, and defecating occurred infrequently (**Table 5**), but were significantly different from chance (aggression: $z = -4.66$, $n = 31$, $p < 0.001$; tail down: $z = -1.79$, $n = 31$, $p = 0.02$; defecating: $z = -2.51$, $n = 31$, $p = 0.003$). Together, this shows that pigs did perceive the test as a stressor.

Pigs paired with a companion with a strong social relationship had a shorter duration of snout proximity and less frequent snout proximity and head proximity (**Table 5**). The social treatment did not influence the frequency of turning or standing alert. Regardless of the social treatment, pigs that attempted to turn more frequently in the crate showed snout proximity less often ($b = -0.26 \pm 0.092$ times; $p = 0.004$). Similarly, pigs that were more often standing alert had less head proximity to the companion ($b = -0.139 \pm 0.062$; $p = 0.03$). Focal pigs that had a female companion had more frequent head proximity than those with a male companion (female companion: 7.13 times, male companion: 5.04 times, SE = 0.241, $p = 0.04$) and tended to have more frequent snout proximity (female companion: 3.22 ± 0.664; male companion: 2.04 ± 0.373, $p = 0.09$). Further, pigs from barren housing conditions were more likely to have snout proximity with the companion than pigs from enriched pens (barren: 3.33 times, enriched: 1.97 times, SE = 0.418, $p = 0.03$).

Table 5. Percentage of pigs (n = 31) that showed each behaviour, and average occurrence of behaviours (LSmeans ± SE, unless reported otherwise) in focal pigs paired with a companion with either a weak or strong relationship, during the 3 minutes of companion presence in the social support test.

Behaviour	%	Weak relationship	Strong relationship	SE	p-value treatment
Standing alert	74.2	1.79	1.93	0.253	0.78
(Attempt to) turn	77.4	2.38	1.59	0.445	0.18
Head proximity	100	7.26	4.95	0.104	0.01
Snout proximity (freq.)	93.5	3.51	1.87	0.122	0.01
Snout proximity (sec.)	100	28.5	11.7	5.73	0.01
Aggression[1]	6.5	0.1 ± 0.28	0.1 ± 0.24	n/a	n/a
Defecating[1]	25.8	0.4 ± 0.51	0.2 ± 0.38	n/a	n/a
Tail down[1]	32.25	0.5 ± 0.51	0.2 ± 0.42	n/a	n/a

[1] Means ± SD

6.4.2 Vocalizations

Pigs (n = 18) made frequent high and low pitch vocalizations, both in the 1 min. solitary phase (mean ± SD high pitch: 2.3 ± 4.80, low pitch: 18.4 ± 9.59), and in the 3 min. social phase (high pitch: 9.9 ± 14.19, low pitch: 37.0 ± 19.32; Fig. 9). In the solitary phase, when the treatment was not yet in effect, pigs from the different treatments did not differ in their frequency of vocalizations ($p > 0.05$; **Figure 9A**), thus confirming that the allocation to the treatments did not give an a priori difference in vocalizations. During the social phase, pigs in the strong social treatment made 2.21 times more low pitch vocalizations than pigs from the weak treatment (strong: 56.5, weak: 25.6, SE = 0.356; $p = 0.002$), but did not differ in the frequency of high pitch vocalizations (strong: 4.03, weak: 10.04, SE = 0.326; $p = 0.26$) (Figure 2a, publication 4). The frequency of low pitch vocalizations further depended on an interaction between social treatment and body weight ($p < 0.001$; **Figure 9B**).

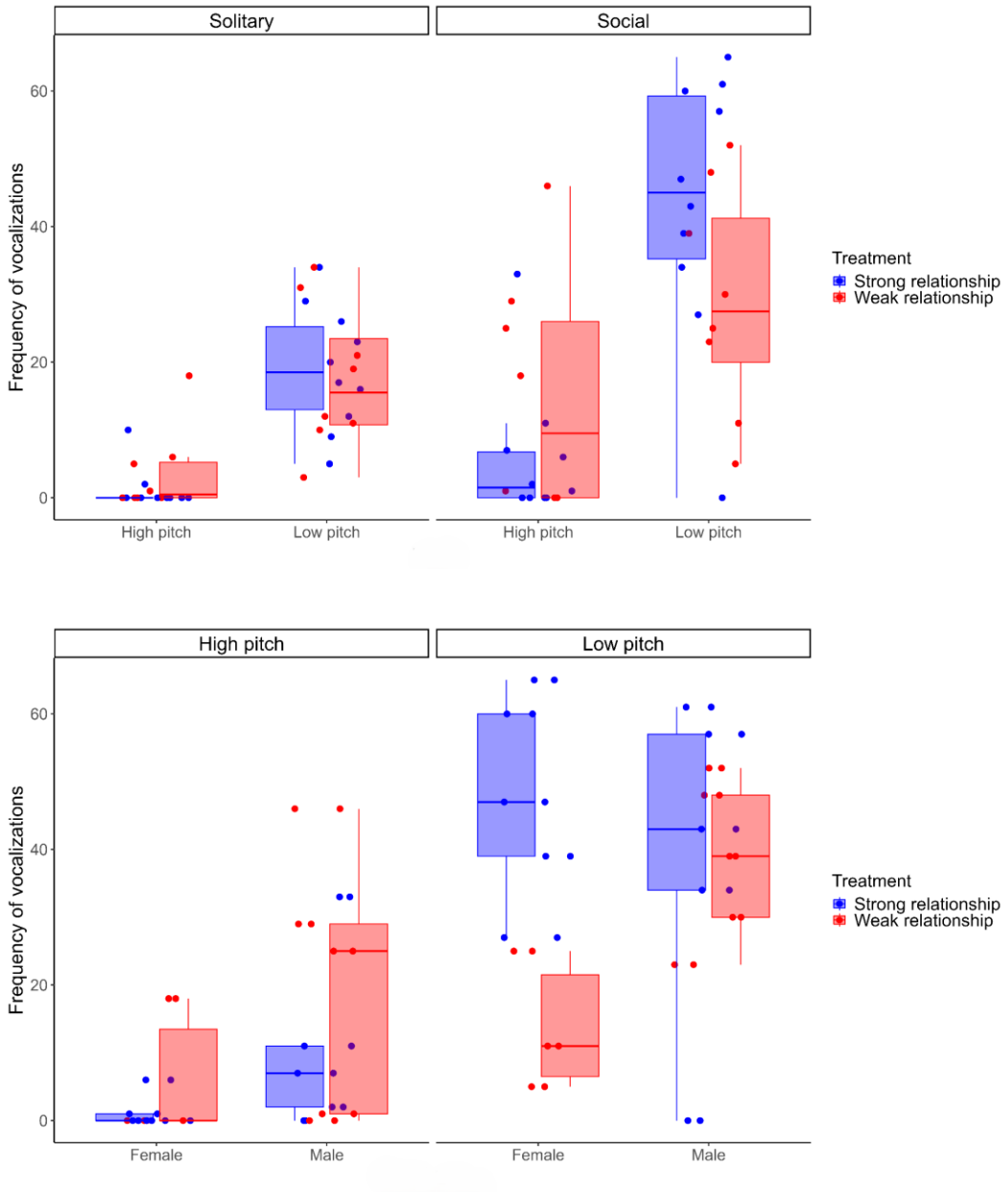


Figure 9. Boxplots showing the effect of the social treatment in focal pigs (n =18). A (top): the frequency of vocalisations in the solitary (1 min.) and social phase (3 min.); B (bottom): the frequency of vocalizations (high and low pitch) in the presence of a companion.

Focal pigs which were paired with a male partner made nine times more high pitch vocalizations than when paired with a female (female partner: 2.07, male partner: 19.58, SE = 0.099; p = 0.01) and 1.5 times more low pitch vocalizations (female partner: 31.5, male partner: 45.9, SE = 3.46, SE = 6.08; p = 0.02; **Figure 10**). Pigs housed in barren housing conditions emitted more low pitch vocalizations compared to pigs from enriched conditions (barren: 45.3, enriched: 31.9, SE = 0.224, p = 0.03).

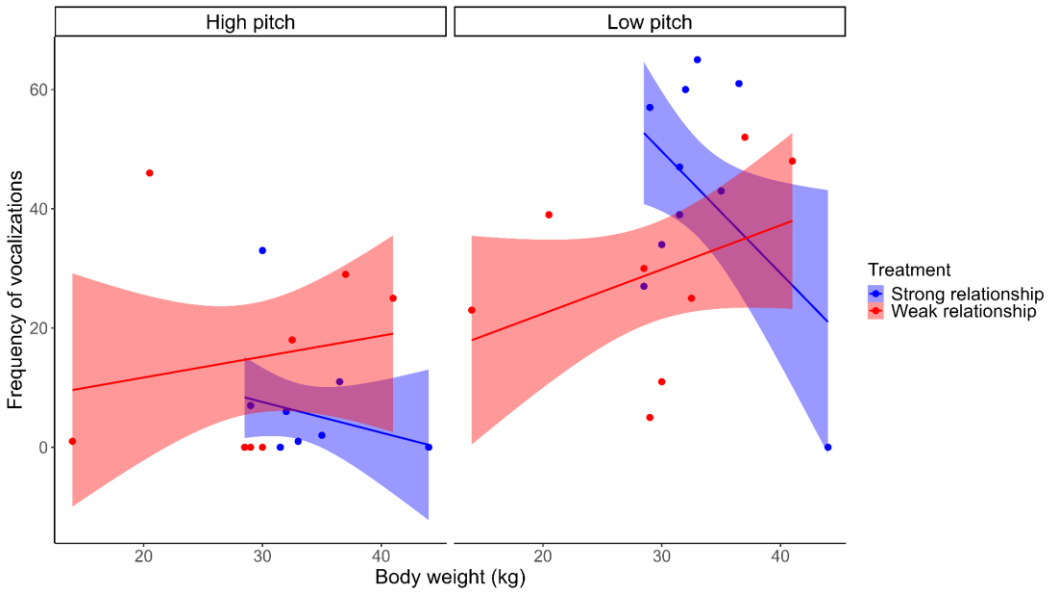
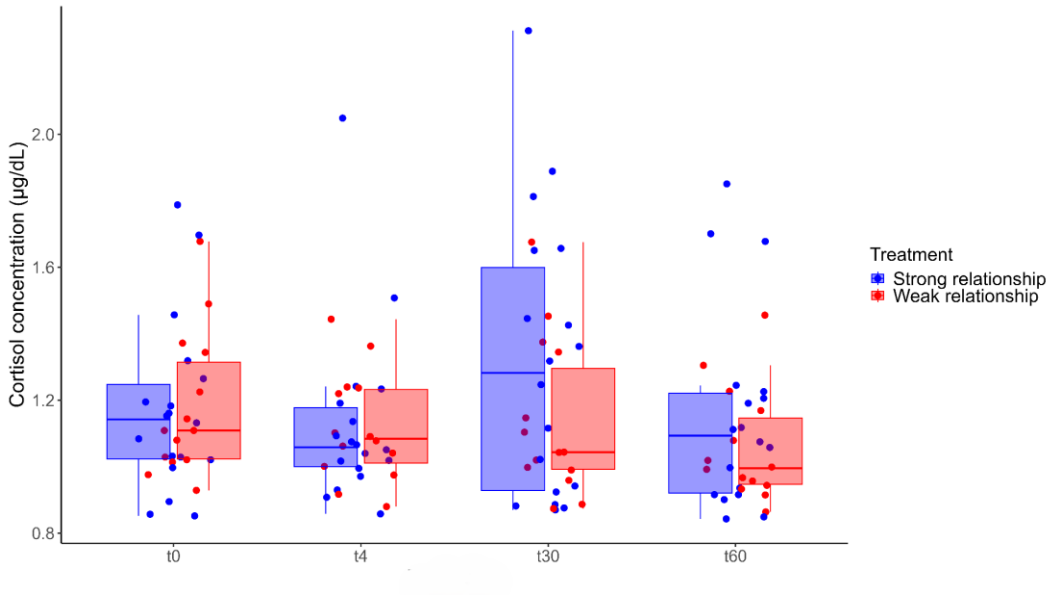


Figure 10. A regression plot showing the differences in interaction between body weight and vocalization due to treatment in focal pigs (n =18).

6.4.3 Cortisol

The saliva cortisol concentrations increased at t30 and reduced by t60 (p = 0.04) but were generally low across the time points (**Figure 11A)**. The social treatment did not significantly influence the proportional change in cortisol concentrations (p = 0.96; **Figure 11B**). The proportional change in cortisol was also not influenced by any of the other predictor values (housing conditions, body weight: p >0.10).



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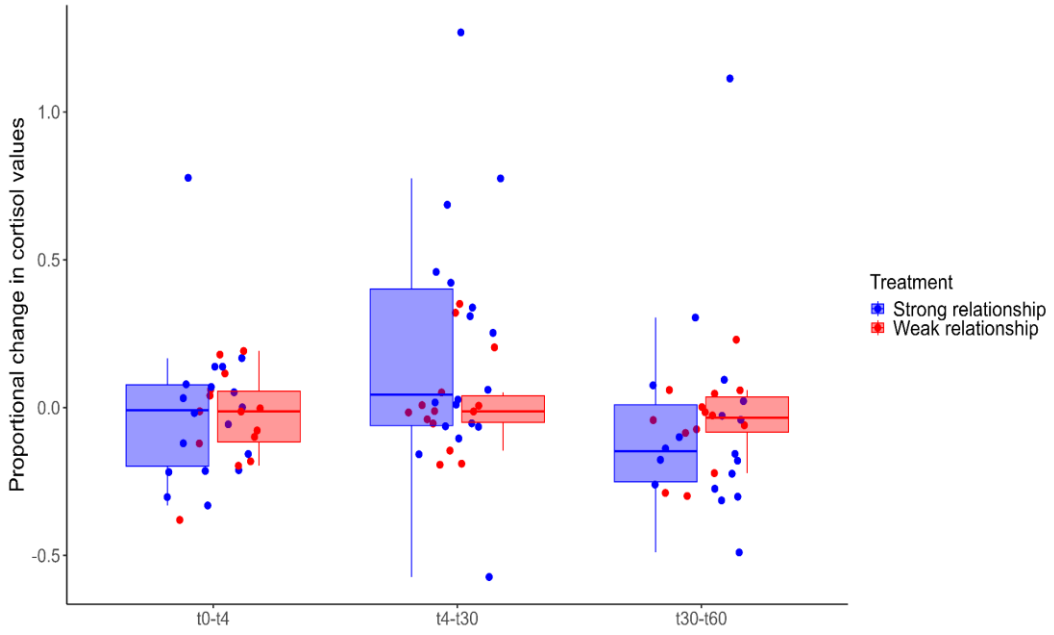

1215

1216 **Figure 11.** Cortisol concentration, A (top): per time point and, B (bottom): per time period
1217 (difference between time points) for focal pigs (n = 31).

1218

6.4.4 The behaviour of the companion

The companions were in nearly all tests scored as calm (83.9%), or otherwise restless (16.1%, n = 5), but were never scored as stressed (0% score 3). Companions varied in the duration that they spent near the crate (mean: 119.1 s; range: 59-168s), which was between 32-93% of the test duration. The proximity of the companion to the crate was not influenced by the social treatment, its sex, housing condition or the behaviour of the focal pig ($p > 0.05$).

6.4.5 Social differentiation

During the regrouping event to test social differentiation, 165 fights were observed in total. The number of fights between unfamiliar pigs (144/165) was above the chance level (proportion test: $\chi2 = 21.22$, df = 1, 95% CI [0.81, 0.91], $p < 0.001$), while fights between siblings kept together occurred below chance level (proportion test: $\chi^2 = 24.34$, df = 1, 95% CI [0.02, 0.09], $p < 0.001$), indicating that pigs avoided fights with siblings from the same pen. However, fights between siblings that had been separated did not differ from the expected chance level (proportion test: $\chi^2 = 0.19$, df = 1, 95% CI [0.04, 0.13], $p = 0.65$). Dyads of siblings that had been separated fought for a shorter duration than unfamiliar dyads, showing that pigs did differentiate between these two categories of familiarity. The other categories of familiarity did not differ from each other in fight duration ($p > 0.05$).

7. General discussion

This dissertation investigated behavioural expressions and traits that contribute to better understanding the social complexity of group-living animals. It focused on three main aspects of social behaviour in pigs, (i) the patterns of social association through snout contact, a key behaviour for maintaining relationships and transmitting social information, and behavioural strategies shaped by subtle individual differences, (ii) the identification and analysis of leadership behaviour, and (iii) the effects of maintaining varying levels of social relationships.

Presented through four publications, the dissertation meets the objectives of the project titled "*The importance of social relationships and social bonds for animals' behavioural expression, health and fitness – pigs as a model to explore the underlying physiological mechanism"*, funded by the National Science Centre (NCN), Poland, project number 2020/39/B/NZ8/02508. Publications 1 and 2 examined factors such as early-life social experience (pre-weaning socialisation), housing conditions, and kinship structure within groups to understand snout proximity and snout contact behaviours. Publication 3 explored the role of early-life coping traits (stress response characteristics) in the development of leadership behaviour. Publication 4 assessed the behavioural and physiological benefits of maintaining social relationships.

Indication of behavioural trade-offs in the expression of snout proximity and contact (Publication 1)

Publication 1 examined how pigs engage in snout proximity and snout contact during social interactions, and considered the potential benefits these behaviours may offer to individuals. As hypothesized, non-tactile snout proximity was most frequent during periods of low social stability and declined as stability increased. Contrary to expectations, tactile snout contact did not show a consistent upward trend over time. Instead, its frequency remained relatively stable, with only a minor reduction observed during the intermediate phase. These findings indicate that snout contact may serve a consistent role in social behaviour, irrespective of changes in group stability. This interpretation is supported by the observed positive association between average daily weight gain (ADWG) and both the initiation and receipt of snout contact, lending support to the hypothesis that this behaviour is linked to individual outcomes in growth.

Following the low stability phase, snout proximity declined, with no notable differences observed between the medium and high stability phases. In contrast, aggression levels were significantly lower only during the high stability phase. This interpretation is further supported by the higher frequency of nosing behaviours among unrelated pigs. Interestingly, even among littermates, nosing behaviour was more frequent during the low stability phase. This pattern aligns with the general increase in social interactions often seen when animals experience changes in their physical or social environment, such as the rise in aggression observed in stable groups following relocation (D'Eath et al., 2010).

An additional hypothesis proposed that snout contact may be linked to individual benefits. A positive association was found between snout contact and body weight gain, although the direction of this relationship remains unclear. It is possible that individuals with higher growth rates have more energy available to engage in social behaviours (Barber, 1991), as has been observed in play behaviour (Brown et al., 2015; Franchi et al., 2023), and they may also be more physiologically equipped to take social risks (Mathot et al., 2015). However, the connection between growth and receiving snout contact suggests that close social interactions may contribute to improved growth outcomes. Previous research has shown that pigs receiving nosing behaviour, which was then observed as contact with any body part, tend to exhibit better growth performance (Camerlink et al., 2012), potentially due to oxytocin release (Uvnäs-Moberg and Petersson, 2005; Camerlink et al., 2012).

Affiliative behaviours in animals are often expressed through physical contact, including allogrooming (Mooring et al., 1998; Tønnesen et al., 2008; Schneider and Krueger, 2012) and licking (Johnsen et al., 2016). In pigs, snout-to-body contact, which may involve nudging or snout-to-snout interaction, is also recognised as a marker of play (Horback, 2023). Snout contact plays a role in strengthening the bond between sows and their piglets (Newberry et al., 1988; Blackshaw and Hagelsø, 1990; Petersen et al., 1990), highlighting its biological relevance. The findings suggest that different forms of nosing, such as snout proximity, snout-to-snout contact, and snout-to-body contact, may serve distinct functions. Similar observations have been made in elephants, where the shape of the trunk during contact is thought to convey different meanings (Yasui and Idani, 2017). Based on the current results, snout proximity appears to be more closely associated

with social recognition, while snout contact may be more indicative of social affiliation. These behaviours may also show contrasting relationships with body weight gain.

Time, and thus the animals' age, presents a natural confound with social stability. However, social behaviour remains largely unaffected by age in juvenile (O'Malley et al. 2022) and sub-adult pigs (Seddaiu et al. 2024) but it can fluctuate depending on the social context (O'Malley et al. 2022). For example, regrouping has a profound effect on the level of aggression (e.g. D'Eath et al. 2010; Turner et al. 2017). In the current study, littermates showed a stable frequency of snout proximity and contact, aside from the low stability phase when they were regrouped with unfamiliar pigs. We can therefore be reasonably confident that the differences in behaviour are related to the level of social stability rather than the change in age.

Network analysis of snout contact behaviour (Publication 2)

Since publication 1 indicated a positive relationship between body growth with snout contact, publication 2 was performed to investigate how pigs re-establish their social relationships, including social preferences, after a regrouping event, and the association pattern of subtle social interactions within this context. When pigs were regrouped into new social groups, a process that typically involves re-establishing dominance relationships to achieve social stability, several group-level metrics within snout contact-based social networks were affected. However, these changes did not significantly alter the overall network structure. Social network analysis conducted during the integration period, based on the frequency of snout contact, revealed several patterns at the group level. In summary, (i) interactions appeared random, without a clear hierarchical organisation; (ii) the network was decentralised, with snout contact distributed across individuals rather than concentrated around a few; (iii) interactions were moderately outward-directed, indicating a general motivation among individuals to engage with others or seek social information; (iv) connections spanned across all group members, forming indirect links; and (v) interactions were heterophilic, occurring more frequently between pigs from different litters and with differing early-life experiences. At the individual level, pigs showed a reduction in the number of social partners over time, as indicated by degree centrality. Despite this decline in unique partners, the frequency of interactions increased in later stages, as reflected by weighted

degree centrality, suggesting more frequent snout contact but with fewer individuals. No consistent or strong partner preferences were observed during any phase of the integration process.

It was expected that snout contact would be frequent during the regrouping of pigs (Jowett et al., 2025), particularly as social stability increased, given its potentially affiliative function. Analysis of the clustering coefficient showed that pigs formed strong social circles based on snout contact during the early stages of group integration, with interactions involving all group members. These interactions declined slightly as integration progressed. Even within small groups of eight pigs, the reduction in social partners suggests a selective approach to social engagement, possibly aimed at acquiring and sharing information (Blumstein et al., 2004).

Social network analysis revealed distinct behavioural roles between males and females. Males were more likely to initiate snout contact, indicating a tendency to actively seek social interaction and increase their frequency of encounters. This aligns with previous findings that male pigs engage more in social behaviours, including nosing and agonistic interactions (Clouard et al., 2022). In natural settings, young males typically leave their family group and live solitarily lives, joining herds only during mating periods, which places them under different social pressures compared to females (Podgórski et al., 2014). Although the males in this study were only four weeks old, prior to puberty and dispersal age (Truvé and Lemel, 2003), earlier research has shown that sex-based differences in social behaviour are evident even at a young age (Brown et al., 2015; Fleming and Dilger, 2017). In contrast, females were more likely to occupy central positions within the snout contact networks, as indicated by eigenvector centrality. This may reflect their inclination to live in sister groups (Podgórski et al., 2014) and their capacity to maintain strong social connections. By associating with well-connected individuals, females may gain access to social benefits such as reduced aggression or stress and improved access to social information (Hasenjager and Dugatkin, 2015; Canteloup et al., 2021). These sex-based differences suggest that underlying socio-biological factors may contribute to variation in individual social behaviour.

The study found that social interactions among pigs were primarily affiliative rather than aggressive. However, no statistically significant social preferences were identified within groups based on snout contact. Previous research involving pigs of a similar age also reported an absence of social preferences when measured through snout contact, although preferences were evident when assessed using lying in contact as a metric (Clouard et al., 2024). While snout contact has

been proposed as a more accurate indicator of affiliative behaviour compared to lying behaviour (Seddaiu et al., 2024) and is increasingly considered suitable for evaluating social relationships (Goumon et al., 2025), it remains uncertain whether snout contact reliably reflects social preferences. Snout-related behaviour (also referred to as social nosing) serves multiple purposes (Camerlink and Turner, 2013), whereby tactile contact is seen as more affiliative (Goumon et al., 2020). However, associations based on spatial proximity may be influenced by environmental factors (Camerlink et al., 2022) and preferences for lying locations (Durrell et al., 2004). For now, the absence of social preferences for snout contact, during any phase of social stability, suggests that young pigs are not socially selective when expressing snout contact.

Although we did not observe pen-directed behaviour, we expect that the difference between the housing conditions is because of the interactions with bedding material rather than with penmates. In more enriched housing conditions, pigs showed a lower likelihood of forming connections with all group members via snout contact, as compared to less enriched housing conditions. From a welfare perspective, the presence of straw, but reduced social contact, is more in line with pigs' natural behaviour as in a semi-natural environment they spent large amounts of time on exploration and little time on social interactions (Stolba and Wood-Gush, 1989). Additionally, the floor space allowance was smaller in the less enriched pens, which may have increased the proximity and likelihood of contact between pigs.

Early life coping styles does not predict leadership (Publication 3)

Factors related to leadership traits in a domesticated population were investigated in Publication 3. The findings from this publication contribute to understanding behavioural traits linked to group movement, like patterns observed in species such as orcas and elephants, where female lineages often play a central role in group leadership, particularly during periods of resource scarcity (McComb et al., 2001; Brent et al., 2015). Leadership involves risk-taking, such as being the first to engage with unfamiliar situations. In the Human Approach Test (HAT), pigs that had not been in contact with humans much demonstrated this by approaching an unfamiliar person, which is typically considered a risky situation (Forkman et al., 2007; Pairis et al., 2009). Latency data showed that many pigs delayed touching the human until the third exposure, indicating that the situation was indeed perceived as risky. Individuals identified as leaders showed notably

shorter latencies compared to followers. However, leadership was only marginally consistent, with just 6 out of 26 groups displaying a single, repeatable leader across three test days.

Publication 3 did not identify any significant links between coping style and leadership, or between body weight and leadership. One possible explanation is that the behavioural traits assessed through the backtest may differ from those observed in the Human Approach Test (HAT), even though both involve responses to perceived threats (Scheffler et al., 2014; Spake et al., 2012). The backtest is commonly used to evaluate coping style in young piglets due to its heritability and consistency over time (Finkemeier et al., 2018; Zebunke et al., 2017) but has faced criticism for its limited alignment with other personality assessments (O'Malley et al., 2019). Despite this, backtest responses have been associated with immune function (Oster et al., 2015) and autonomic nervous system activity during general behaviour and human interaction (Krause et al., 2017). Krause and colleagues found that pigs classified as reactive in the backtest, those showing minimal resistance, took longer to approach and touch a familiar human than proactive pigs, though this pattern was only evident during the initial three days of testing. These findings suggest that the influence of coping style may vary depending on context and age.

Interestingly, females were more frequently observed in leadership roles than males. Although the pigs were still young (6 weeks of age), previous research has shown that juvenile female wild boar can form social groups even in the absence of adult females (Bieber et al., 2019), indicating that leadership can emerge among group-living females. While adult and sub-adult pigs exhibit clear physical and behavioural differences between sexes (Konjević et al., 2008; Camerlink et al., 2022), such distinctions are subtle in young pigs. Therefore, the higher occurrence of leadership among females was unexpected. Based on the larger body size of males and their dominant behaviour in conflict situations (Camerlink et al., 2022), it was anticipated that males would more often assume leadership roles. However, the observed pattern aligns with wild populations, where mature female wild boar typically lead small herds (Podgórski et al., 2014), while males tend to live solitarily lives apart from the breeding season (Maselli et al., 2014). Variation in leadership is common across species, suggesting that leadership roles may be shaped by context. This raises the possibility that pigs engage in distributed leadership, where roles are shared among individuals rather than held by a single leader (Leca et al., 2003). However, it may also be that leadership is weakly developed in young pigs.

Behaviour during social support partly mediated by relationship strength (Publication 4)

Publication 4 explored the potential benefits of maintaining social relationships by examining whether behavioural and physiological responses to a stressor were influenced by the strength of the relationship between the focal pig and its companion. It was hypothesised that dyads with a strong social relationship, created by continuously housing siblings together, would show reduced stress responses compared to dyads with a weaker social relationship, created by separating siblings for at least two months. During the solitary phase of the social support test, pigs displayed mild behavioural signs of distress, which diminished when the companion entered the arena. Although the presence of a social partner led to observable behavioural changes, it did not result in a measurable reduction in physiological stress, as indicated by salivary cortisol levels.

It was expected that pigs in the strong social relationship condition would exhibit fewer stress-related behaviours, such as turning in the weigh crate and standing alert. However, these behaviours were not significantly affected by the treatment, and behaviours such as aggression, tail down, and defecation occurred too infrequently to analyse. Somewhat similar findings were reported by Reimert et al. (2013), who observed no differences in freezing, defecation, or tail posture in pigs exposed to aversive or rewarding stimuli, although differences emerged during training phases. The most notable behavioural differences were found in the frequency and duration of social proximity. Snout proximity, which is associated with social recognition (Newberry and Wood-Gush, 1986; Camerlink and Turner, 2013), typically increases when unfamiliar pigs meet (Camerlink et al., 2022). Pigs with a strong relationship engaged in less snout and head proximity and spent less time in close contact. Although it was anticipated that pigs with a stronger relationship would have more contact, the reduced proximity may reflect their familiarity. In the weak relationship treatment, the pigs had not interacted for two months, likely increasing social interest (Ewbank and Meese, 1971). Other studies have similarly found that unfamiliar pairs show more proximity (Söderquist et al., 2023) or contact (Kanitz et al., 2014), possibly due to mixed motivations such as curiosity or aggression (Söderquist et al., 2023). Previous studies have shown that social support is less effective when provided by unfamiliar pigs (Kanitz et al., 2014; Söderquist et al., 2023). The duration of fights with separated siblings was

shortest, suggesting that pigs retained some recognition of their siblings, possibly through olfactory cues (Kristensen et al., 2001), even after a separation of at least two months.

During the social phase, pigs in the strong social treatment produced more low-pitched vocalisations than those in the weak treatment, while no difference was found in high-pitched vocalisations. Vocalisations of different pitch are associated with varying emotional contexts (Briefer et al., 2022). High-pitched sounds, such as screams, squeals, and grunt-squeals, are typically linked to stressful situations (Reimert et al., 2013), whereas low-pitched vocalisations, including short and long grunts, serve multiple communicative purposes (aversive events: Reimert et al., 2013; positive contexts: Maigrot et al., 2018). The findings suggest that the strength of the social relationship influenced overall communicative behaviour. Taken together, the results refute the hypothesis that the relationship strength affects social support.

Focal pigs vocalised more when the companion was male rather than female. As the males were at their onset of puberty, they may have shown increased interest in the female in the crate. Boars are known to produce frequent grunts during sexual behaviour (Hemsworth and Tilbrook, 2007), which may have influenced the vocal responses of the females. Heavier pigs in the strong relationship treatment produced fewer low-pitched vocalisations, whereas heavier pigs in the weak bond condition vocalised more. Heavier individuals may hold a higher dominance status (Drickamer et al., 1999), although this is not always the case (Tong et al., 2019), and dominance may influence communication strategies depending on the social context (Seyfarth and Cheney, 2003; Nogueira et al., 2016).

Cortisol concentrations peaked at the 30-minute sample and declined thereafter, indicating a physiological stress response consistent with findings from other studies using salivary cortisol in pigs (e.g., Reimert et al., 2014; Escribano et al., 2015). However, no significant effects of treatment or other variables were found on cortisol concentrations. This aligns with the findings of Reimert et al. (2014), who also reported behavioural differences without corresponding changes in salivary cortisol in a social support test. The current study followed a similar sampling protocol, with the main difference being the duration of stress exposure, four minutes in this study compared to fifteen minutes in Reimert et al. (2014), a decision made for welfare reasons. The shorter exposure may have been insufficient to produce detectable physiological differences between treatment groups.

Pigs are known to be sensitive to the emotional states of others and may respond to a distressed peer with increased proximity or freezing behaviour (Goumon and Špinka, 2016). Although emotional contagion has been proposed as a mechanism for facilitating social support in animals (Ben-Ami Bartal et al., 2016; Peen et al., 2021), recent findings in pigs suggest that emotional contagion in the observer does not necessarily enhance the effectiveness of social buffering (Reimert and Bolhuis, 2024). It is possible that more intense distress, such as that induced by electric shocks (Zhang et al., 2023), or prior experience with the stressor (Goumon and Špinka, 2016), may be required to elicit stronger social support responses. Another caveat is that such emotional state could affect the behaviour of the companion. Further research into pigs' ability to recognise emotional states and engage in empathy-like behaviours (Marino and Colvin, 2015) may help clarify the mechanisms involved.

8. Conclusion

Subtle social behaviours and their implications for social relationships were explored, along with the effect of other factors such as early life social experiences. The results from these studies led us to conclude that,

1. the observed positive association between snout contact and body weight gain, together with the negative association between snout proximity and body weight gain, suggests the occurrence of behavioural trade-offs in a low social stability context. Individuals with slower growth, who may be more vulnerable to the costs of increased physical interactions, appear to adopt non-tactile behaviours such as snout proximity to avoid direct contact. In contrast, snout contact is associated with better growth performances. These findings suggest that during group formation, snout proximity may function primarily in conflict avoidance and recognition of conspecifics, while snout contact may play a more affiliative role in social association.

2. though snout contact has been proposed as a more reliable indicator of affiliative behaviour than spatial proximity during lying, and is increasingly considered suitable for assessing social relationships (Goumon et al., 2025), social preferences based on this behaviour were not found. The absence of such preferences across different phases of social stability suggests that young pigs may not be socially selective when associating in snout contact.

3. the observed sex-based differences in leadership behaviour provide insight into the social structure of domestic pigs, suggesting that leadership may be influenced more by socio-biological factors than by early developmental traits as there was no clear association between coping styles or body weight and the likelihood of pigs assuming a leadership role in a novel situation.

4. the strength of social relationships, as determined by close familiarity, was found to influence pig behaviour during stressful situations, particularly in terms of social proximity and low-pitched vocalisations. Recognizing the role of social relationship strength can enhance both the validity of behavioural research and the welfare of the animals involved.

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10. Appendices

10.1 Author's contribution to each publication

I hereby give each author's contribution to the publication:

Khatiwada, S., Lee, V., Turner, S.P., Camerlink, I. (2025). Trade-offs between proximity and physical contact during group integration in pigs (*Sus scrofa domesticus*). *Current Zoology.*

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Khatiwada, S., Lee, V., Turner, S.P., Camerlink, I. (2025). Temporal social network structures based on snout contact during group integration in pigs. *Applied Animal Behaviour Science.*

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Khatiwada, S., Turner, S. P., Farish, M., & Camerlink, I. (2024). Leadership amongst pigs when faced with a novel situation. *Behavioural Processes*, *222*, 105099.

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Khatiwada, S., Seddaiu, P., Jaszczyk, A. & Camerlink, I. (2025). Is social support mediated by social relationship strength in pigs? animal.

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10.2 Publications

Current Zoology, 2025, **00**, 1–9
https://doi.org/10.1093/cz/zoaf056
Advance access publication 18 August 2025
Original Article

Trade-offs between proximity and physical contact during group integration in pigs (*Sus scrofa domesticus*)

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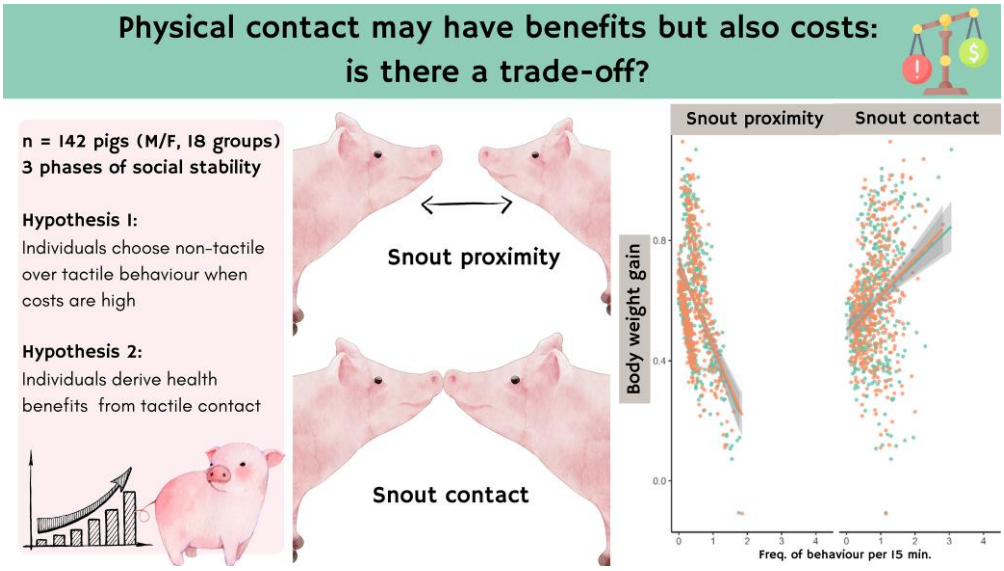
Handling editor: Zu-Shi Huang

Abstract

During behavioral trade-offs, individuals have to decide whether to express a behavior which may lead to a reward or potential costs when engaging in a risky situation. Social integration forces animals to make such trade-offs. We hypothesized that animals predominantly demonstrate nontactile behavior and hence less tactile behavior in a high-risk context such as during social integration, while using tactile behavior more than nontactile in less risky situations such as under social stability. Pigs (*Sus scrofa domesticus*) typically are in close physical contact to each other, but physical contact also relates to increased aggression. We investigated 18 groups (142 pigs) across different phases of social stability, thereby observing snout proximity and snout contact. Additionally, aggression (reflecting costs) and growth performance (reflecting benefits) were measured. Data were analyzed using mixed models while accounting for group stability. Snout proximity was indeed most frequent during social instability and reduced as stability increased, while snout contact remained more constant. The high occurrence of snout proximity during social instability suggests conflict avoidance and thus risk aversion. Animals that showed more frequent snout proximity grew slower, while initiators and recipients of frequent snout contact had a better growth performance. The causality of these effects cannot be ascertained, but it is possible that slower growing, and thus weaker individuals may have made a behavioral trade-off by choosing proximity rather than contact during social instability. The results further emphasize the importance of distinguishing between nuances in behavior.

Key words: aggression, behavioral trade-offs, group dynamics, social behavior, social nosing, *Sus scrofa*.

Graphical Abstract



Received: 30 September 2024; accepted: 15 August 2025

Behavioral expression, a signaling process that transmits information from initiators to recipients (Demartsev et al. 2023), can assist social members in various scenarios, such as in recognizing group members and maintaining social relationships. Animals are expected to balance the costs and benefits from decisions in any given context (Vázquez et al. 2020; Carsten et al. 2023) and attempt to initiate interactions via a signaling process that can reduce costs (Tibbetts and Dale 2007). To transmit information, group-living animals have developed different forms of communication, such as nontactile (e.g., olfactory and vocal) and tactile contact (e.g., physical aggression), of which some may pose more risk than others.

Tactile behavior is common in many species' behavioral repertoire, such as muzzle contact in vervet monkeys (*Chlorocebus pygerythrus*) (Nord et al. 2021), post-conflict affiliative muzzle contact in domestic goats (*Capra hircus*) (Schino 1998), reconciliatory contact in mandrills (*Mandrillus sphinx*) (Schino and Marini 2011), and mouth–mouth interaction in beluga calves (*Delphinapterus leucas*) (Hill et al. 2019). Individuals derive benefits from tactile behavior throughout life as it contributes to the maintenance and formation of social bonds (Uvnäs-Moberg 1998). Gentle tactile behavior is argued to serve a function in regulatory, affiliative and communicative processes (Gliga et al. 2019) and increases endogenous oxytocin secretion contributing to health and development (Uvnäs-Moberg 1998) including growth (Uvnäs-Moberg and Petersson 2005; Champagne et al. 2008). However, tactile behavior can also lead to aggression which may have serious consequences, and therefore nontactile contact may in some contexts be preferred to minimize risks of injury. It is therefore beneficial for social species to engage in their relevant species-specific gentle tactile behavior (e.g., allogrooming, snout contact, licking) or nontactile behavior depending on the situation.

Given the potential costs and benefits of tactile behavior, it is of great importance for the individuals of social species to be able to switch between tactile and nontactile behavior. Switching between tactile and nontactile behavior, and adopting the strategy that bears the least risk can provide benefits such as increased information gathering (Partan and Marler 2005). This may be particularly important during risky situations, such as during a time of social instability where both the potential costs (Prevolnik et al. 2021) and benefits of tactile behavior may be increased. The establishment of new social groups, resulting in social instability, is in domestic pigs a common occurrence due to the way they are managed (Coutellier et al. 2007). Pigs form dominance relationships (McGlone 1985) and use, amongst others, olfactory signals for social recognition (Kristensen et al. 2001). For this they require to be in close proximity because of the functioning of the vomeronasal organ (VNO) (Schild and Rørvang 2023). It has been proposed that nontactile snout proximity relates to social recognition while tactile snout contact relates at least in part to affiliative behavior and may benefit the recipient's health in the form of an increased growth performance (Camerlink et al. 2012; Camerlink and Turner 2013). However, it may also risk the costs of receiving aggression.

The objective of this study was to investigate the occurrence of snout proximity and snout contact during social encounters in pigs, while exploring the costs and benefits individuals may accrue from these behaviors. We hypothesized that pigs demonstrate more nontactile snout proximity in a situation where the associated costs of direct contact are high, and express tactile snout contact when the situation is less risky. We predict more nontactile snout proximity behavior when the risks are high, which is in the early stage of group integration when there is frequent aggressive behavior, and that it reduces with increasing group stability (prediction 1). At the same time, we predict that tactile snout contacts increase with increasing social stability (prediction 2), as evidenced through low aggression. Further, we hypothesize that these behaviors will relate to individual costs and benefits in terms of growth performance. If true, then subtle differences in social behavior (proximity versus contact) can have opposite outcomes for growth performance and will be important to consider in the study of animal behavior.

Materials and Methods

Animals and housing

Male ($n = 72$) and female pigs ($n = 70$) (Large White × Landrace sows × Danish Duroc boars) ($n = 18$ groups) were studied on the Easter Howgate Pig Research Unit across three batches (i.e., cohorts), starting when animals were 4 weeks of age. Approximately half of the piglets (10–14 days old) were socialized preweaning by allowing two litter groups to mingle (the piglets could interact, but the sows could not) through an opening between two farrowing pens before the start of the experiment. The experiment started when pigs (4 weeks of age) were weaned from the sow and transferred to another research building. Here, different sibling groups were combined to form new social groups. Groups were composed of eight pigs (males and females) from two different litters unfamiliar to each other (four siblings per litter), thereby resulting in each pig being housed with three familiar and four unfamiliar pigs. The sex ratio and number of socialized pigs per group were balanced where possible but due to variation in birthdate and number of males and females this deviated from a 1:1 ratio in approximately half of the groups. The groups were either housed in enriched conditions ($n = 9$ groups; pen of 6.9 m × 2.1 m, with deep straw bedding, Porcichew pig toys and hessian ropes) or in less-enriched conditions ($n = 9$ groups; pen of 4.6 m × 2.1 m, with rubber mats and wood shavings but no straw or toys). All pigs within a group were exposed to the same housing condition. Sibling groups were balanced across housing conditions. Pigs were fed ad libitum commercial pig feed and had water available via nipple drinkers. All pigs were weighed regularly, and average daily weight gain (ADWG) in kg per day was calculated for week 4–5 of age, week 6–8 and week 10–11, where ADWG = (weight last week – weight first week)/days between weeks. To enable individual identification, pigs were ear-tagged and received a spray mark on their back with animal marker spray. In the course of the observation period, three individuals were taken off trial and removed from the observed groups due to health issues.

Behavioral observations

The behaviors snout proximity, snout contact and aggressive behavior were recorded following the ethogram in Table 1, while noting both the initiator and recipient. When an initiator approached and made contact to a recipient within <1 s, the behavior was scored as snout contact without scoring snout proximity separately. Behavioral observations were conducted on all pigs from week 4 until week 11 (without observation in week 9) using continuous behavioral sampling live and from video (Bateson and Martin 2021). Each group was observed

continuously for 15 min per session, with 3–4 observation sessions per day. This resulted in 45 min to 1 h of continuous observation per group per day. Each study week included two observation days (except week 4 in which 3 days were observed), resulting in 2 h of observations per group per week. Observations were randomized and done across 7 weeks (resulting in ca. 14 h of observations per group). The behaviors were recorded by a single observer, using the "Animal Behavior pro" application installed on an ipad mini 2.

Dominance relationships

From the overall frequency of aggressive interactions, the Modified David Score (MDS) was calculated as an indicator of dominance rank. The Modified David Score is an adaptation of the original David's Score, which is a method used to rank individuals in a social group based on their dominance interactions. The MDS was calculated using the "steepness" package (version 0.3-0) (Leiva and de Vries 2022) in R (version 4.3.2) (R Core Team 2023). Due to the relatively infrequent occurrence of aggression in some weeks, dominance relationships could not be reliably calculated by week (to show the change over time) and were instead calculated across the whole observation period.

Social stability

From literature it is well-known that pigs at regrouping show a peak of aggression, after which there is a gradual reduction in agonistic interactions across the 3 weeks following (Meese and Ewbank 1973; Prevolnik et al. 2021). Therefore, observation weeks were chosen at different stages of group stability. Weeks 4–5 of age (weeks 1–2 after regrouping) represents social instability as they will need to form new dominance relationships (Meese and Ewbank 1973; McGlone 1985). Weeks 6–8 of age (weeks 3–5 after regrouping) represents medium social stability, as most dominance relationships will have formed but some changes in hierarchy may still occur (Meese and Ewbank 1973). Weeks 10–11 of age (weeks 7–8 after regrouping) represents high social stability.

As aggression was too low in some weeks to calculate the stability of dominance positions, we verified the stability of the phases by the frequency of aggression. Analysis of differences in aggression between the social stability phases was conducted using a mixed model with aggression as response variable, phase as predictor variable and batch as random variable. This showed that the low and medium stability phases had significantly more aggression than the high stability phase (low vs. high: $P < 0.001$, medium vs. high: $P < 0.001$) (Figure 1). The low and medium stability phase did not significantly differ ($P = 0.23$; Figure 1) but were kept separate as the early phase contains higher outliers and keeping them separate aligns with the time required for dominance establishment as reported in the literature (Meese and Ewbank 1973). Data for behavior and average daily weight gain (ADWG) were therefore divided into these three phases for social stability: low (weeks 4–5 of age), medium (weeks 6–8 of age) and high (weeks 10–11 of age).

Data analyses

There was a moderate correlation between initiating and receiving behaviors, both for snout proximity ($r = 0.31$, $P < 0.001$), snout contact ($r = 0.38$, $P < 0.001$), and aggressive behavior ($r = 0.32$, $P < 0.001$) (Cor.test function). This suggests that individuals who initiate these behaviors are also the recipients of the behavior, as the behavior may be reciprocated. Based on the correlation, we included only information from the initiator in analyses of social behavior while taking into account both initiators and recipients for the association with ADWG. Additionally, correlation analysis was performed between MDS and ADWG, and between aggressive behavior and snout proximity, and snout contact. The correlation was performed using the "cor.test" function in R. Not all animals had the same amount of observations, and therefore the behaviors were divided by the total number of 15-min sessions per animal to come to an average frequency per 15 min.

Table 1. Ethogram of observed behaviors in 4–11 weeks old pigs ($n = 142$).

Behavior	Description
Snout proximity	Pig proactively brings its snout within 30 cm distance of the snout of another pig, by turning its head towards the other, without making contact (irrespective of the duration).
Snout contact	Pig proactively touches the snout (area below the eyes, including nose disc) of another pig with its nose disc (irrespective of the duration).
Aggression	Pig delivers a head knock, threat, push, and/or bite to another pig, or engages in a mutual fight, including a rapid sequence of biting. Can include moments in which the opponents stand still (pause) to regain breath. Continues until one retreats or until other behavior (excl. standing still) is performed for at least 3 s.

We performed three linear mixed models in R using the package lmerTest (version 3.1-3) (Kuznetsova et al. 2017). In model 1, the response variable was the frequency of snout proximity or frequency of snout contact per session (two separate analyses). The predictor variables were social stability phase, housing condition, socialization, sex, and MDS. The random variables were batch and pig ID nested within group. In model 2, ADWG was the response variable (for the initiator and recipient separately). The predictor variables were snout proximity, snout contact, aggression, housing condition, socialization, and sex, with as random variables batch and pig ID nested within group. In model 3, the frequency of snout proximity and snout contact towards related (littermates) and unrelated conspecifics (nonlittermates) was analyzed in a mixed model. The response variable was the frequency of snout proximity or snout contact (two separate analyses). The predictor variables were housing condition, sex, socialization, and social stability, with as random variables pig ID and group nested within batch.

We selected the best fit model based on lowest AIC value after backward selection on the full model using the function step(). Due to the backward selection step the final model had only the variables that best fitted the model. Hence in model 1, the phase of social stability, housing condition and sex best predicted snout proximity behavior whereas phase of social stability, housing condition and MDS best predicted the snout contact behavior. In model 2, snout proximity and snout contact best predicted the ADWG for initiator whereas, snout proximity, snout contact, and aggressive behavior was in the final model for recipient. In model 3, the phase of social stability, housing condition, and individual sex best fitted the model for snout proximity towards unrelated individuals. In contrast, only the phase of stability and housing condition

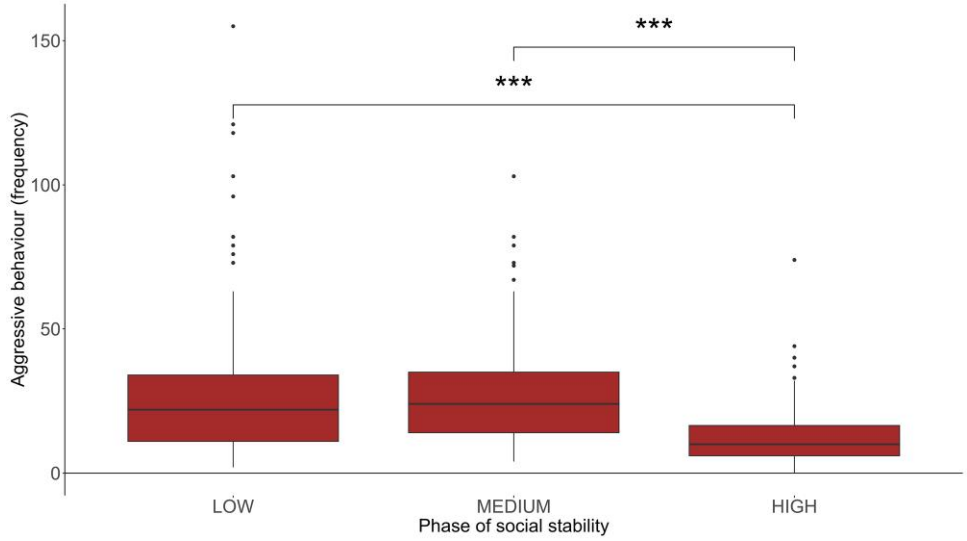


Figure 1. Frequency of aggressive behavior, based on behavioral observations of agonistic behavior as described in Table 1, across phases of social stability: low stability (1–2 weeks after regrouping, 4–5 weeks of age), medium stability (3–5 weeks after regrouping, 6–8 weeks of age), and high stability (7–8 weeks after regrouping, 10–11 weeks of age).

was in the final best fit model for the snout proximity towards related individual. Similarly, the phase of social stability and housing only best fitted the model for snout contact towards unrelated as well as related conspecifics. Model diagnostics were performed on the best fit model to check for normality and homogeneity of residuals and collinearity between predictor variables. Residuals were normally distributed, as assessed from Shapiro–Wilk statistics. Homogeneity was validated by visual inspection of residual plots against fitted values from sjPlot package (version 2.8.15) (Lüdecke 2024). Cook distances were calculated and plotted to identify influential data points (the Cook distance for any data point was smaller than 1 in all models). The variance inflation factor was performed to detect multicollinearity (i.e., correlation between predictor variables) from the "car" package (version 3.1-2) (Fox and Weisberg 2018). The variance inflation factor did not indicate strong multicollinearity (<2). Post hoc analyses were performed using the "emmeans" (version 1.8.9) package (Russell 2020) to report least square means (LSmeans) with standard errors (SE). Reported values are LSmeans with SE unless stated otherwise. P values were obtained for the model and considered significant at ≤ 0.05. Figures were made using the "ggplot2" package (version 3.5.1) (Wickham 2016).

Results

Hypothesis 1: Individuals choose nontactile over tactile behavior when risks are high

We predicted that pigs would show snout proximity when costs (in terms of aggression) are high and show more snout contact when risks are low. Pigs showed, on average, 0.46 ± 0.33 (means $\pm$ SD) times snout proximity per pig per 15 min, and 0.82 ± 0.48 times snout contact per pig per 15 min. The frequency of snout proximity differed depending on social stability (low–mid: 030 ± 0.026; low–high: 030 ± 0.026; $P < 0.001$, model 1), with the highest frequency during low social stability, while there was no significant difference between the medium and high stability phase (Figure 2). The frequency of snout contact was lower during the medium stability phase (low–mid: 0.10 ± 0.039, $P = 0.02$; MID–HIGH: -0.13 ± 0.040, $P = 0.002$, model 1) while being numerically but not significantly higher in the phase of high social stability (Figure 2). There was a positive correlation between snout proximity and snout contact in all phases of social stability (low: $r = 0.75$, $P < 0.001$; medium: $r = 0.52$, $P < 0.001$; high: $r = 0.61$, $P < 0.001$).

Aggressive behavior was positively correlated with snout proximity (r_{range}: 0.34–0.65; $P < 0.001$) and snout contact (r_{range}: 0.4–0.66; $P < 0.001$) across the phases of social stability. The Modified David score (MDS) did not relate to the expression of snout proximity ($P = 0.42$; model 1) but did relate to the expression of snout contact ($b = 0.006 \pm 0.002$; $P = 0.03$; model 1) indicating that pigs with higher dominance value initiated more snout contact. There was no correlation between dominance (MDS) and weight gain (ADWG; $r = 0.01$; $P = 0.89$). Males expressed more snout proximity than females (males: 0.54 ± 0.126; females: 0.46 ± 0.126 times/15 min; $P = 0.002$) but did not differ from females in the frequency of snout contact ($P = 0.48$). Pigs in the more enriched housing conditions showed less frequent snout proximity (enriched: 0.46 ± 0.114 times/15 min vs. less-enriched: 0.52 ± 0.114 times/15 min; $P = 0.02$, model 1) and snout contact (enriched: 0.81 ± 0.184 times/15 min vs. less-enriched: 0.94 ± 0.184 times/15 min; $P = 0.01$, model 1) than the less-enriched pigs. Preweaning socialization did not influence the snout proximity ($P = 0.80$) or contact ($P = 0.65$).

Hypothesis 2: Individuals derive benefits from tactile contact

Pigs that initiated or received a greater frequency of snout proximity had a lower average daily weight gain (ADWG) than those who did so less (initiator: $b = -0.65 \pm 0.056$ kg/day; $P \leq 0.001$; recipient: $b = -0.62 \pm 0.060$ kg/day; $P \leq 0.001$; model 2) (Figure 3). In line with our hypothesis, frequent initiators and recipients of snout contact had a greater ADWG than those who initiated or received less snout contact (initiator: $b = 0.20 \pm 0.041$ kg/day; $P \leq 0.001$; recipient: $b = 0.18 \pm 0.046$ kg/day; $P \leq 0.001$; model 2) (Figure 3). To confirm the costs associated with aggression, pigs that

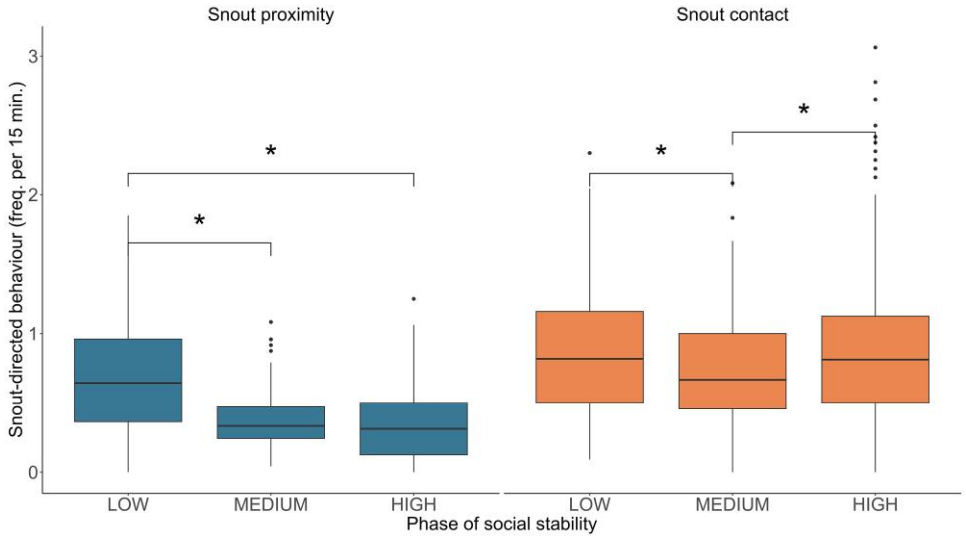


Figure 2. Average frequency (per pig per 15 min of observation) of snout proximity (left) and snout contact (right) by phase of social stability. The asterisk indicates significant differences ($P < 0.05$) between the phases.

received more aggressive behavior had a lower ADWG ($b = -0.11 \pm 0.030$ kg/day; $P \leq 0.001$; model 2) whereas for the initiator aggression was not significantly associated with ADWG ($P = 0.43$).

Factors affecting snout proximity and contact

Unrelated conspecifics showed more snout proximity towards each other compared to related conspecifics (nonlittermates: 0.31 ± 0.013, vs. littermates: 0.24 ± 0.077, $P < 0.0001$) and more snout contact (nonlittermates: 0.31 ± 0.077 vs. littermates: 0.24 ± 0.077, $P < 0.0001$). In the phase of low social stability, related pigs (littermates) showed more frequent snout proximity towards each other than in the later phases ($P < 0.001$, model 3; Figure 4).

Discussion

As hypothesized, nontactile snout proximity was highest during low social stability and reduced with increasing social stability. However, unexpectedly, tactile behavior in the form of snout contact did not show a linear increase over time as we predicted. Instead, snout contact remained reasonably constant, with only a slight decrease in the intermediate phase. This suggests that snout contact is an important behavior regardless of social stability. This is supported by the positive relationship between body weight gain (ADWG) and the initiation and receipt of snout contact, which aligns with our second hypothesis that snout contact translates into individual costs and benefits in growth.

Snout proximity reduced after the low stability phase, with no significant difference between the phases of medium and high social stability, while aggression was significantly lower only in the high stability phase. This suggests that snout proximity mostly serves a function in social recognition (Penn and Frommen 2010). This is further confirmed by the more frequent nosing behaviors between the unrelated pigs. However, even between littermates nosing behavior was higher in the low social stability phase, although an increase in interactions is common during a change in the physical or social environment (e.g., increased aggression is seen in stable groups when they are relocated; D'Eath et al. 2010).

We further hypothesized that snout contact would relate to benefits. We indeed found a positive correlation between snout contact and body weight gain, although here as well, the directionality of the effect is uncertain. Individuals with better growth may have more energy to invest in social relationships (Barber 1991), as is reported for play behavior (Brown et al. 2015; Franchi et al. 2023), and they may have physiological advantages when taking risks (Mathot et al. 2015). However, the relationship between growth performance and the receipt of snout contact suggests that close interactions are associated with faster growth. Previous studies have shown that recipients of nosing behavior (contact with any body part, without distinction between snout proximity and contact) had a better growth performance (Camerlink et al. 2012), which is suggested to occur through the release of oxytocin (Uvnäs-Moberg and Petersson 2005; Camerlink et al. 2012). Animals can express their affiliative behaviors using body contact, allogrooming (Mooring et al. 1998; Tønnesen et al. 2008; Schneider and Krueger 2012), and licking (Johnsen et al. 2016). Snout-to-body contact, which may include nudging and snout-to-snout contact, is also used as a play marker (Horback 2023). Snout contact specifically can consolidate the social bond between the sow and her piglets (Newberry et al. 1988; Blackshaw and Hagelsø 1990; Petersen et al. 1990) and is therefore a biologically relevant behavior for pigs. The results show that the differential use of nosing behavior such as snout proximity, snout-to-snout contact and snout-to-body contact can have different implications for individuals. Similarly, Yasui and Idani (2017) have argued that for elephants the shape of the trunk when touching other conspecifics implies different functions. Based on the current results, we suggest that snout proximity is used more for social recognition whereas snout contact may relate more to social affiliation, and that these two behaviors may have an inverse relationship with body weight gain.

In social species which maintain a dominance hierarchy, dyadic encounters determine their rank order, which can be

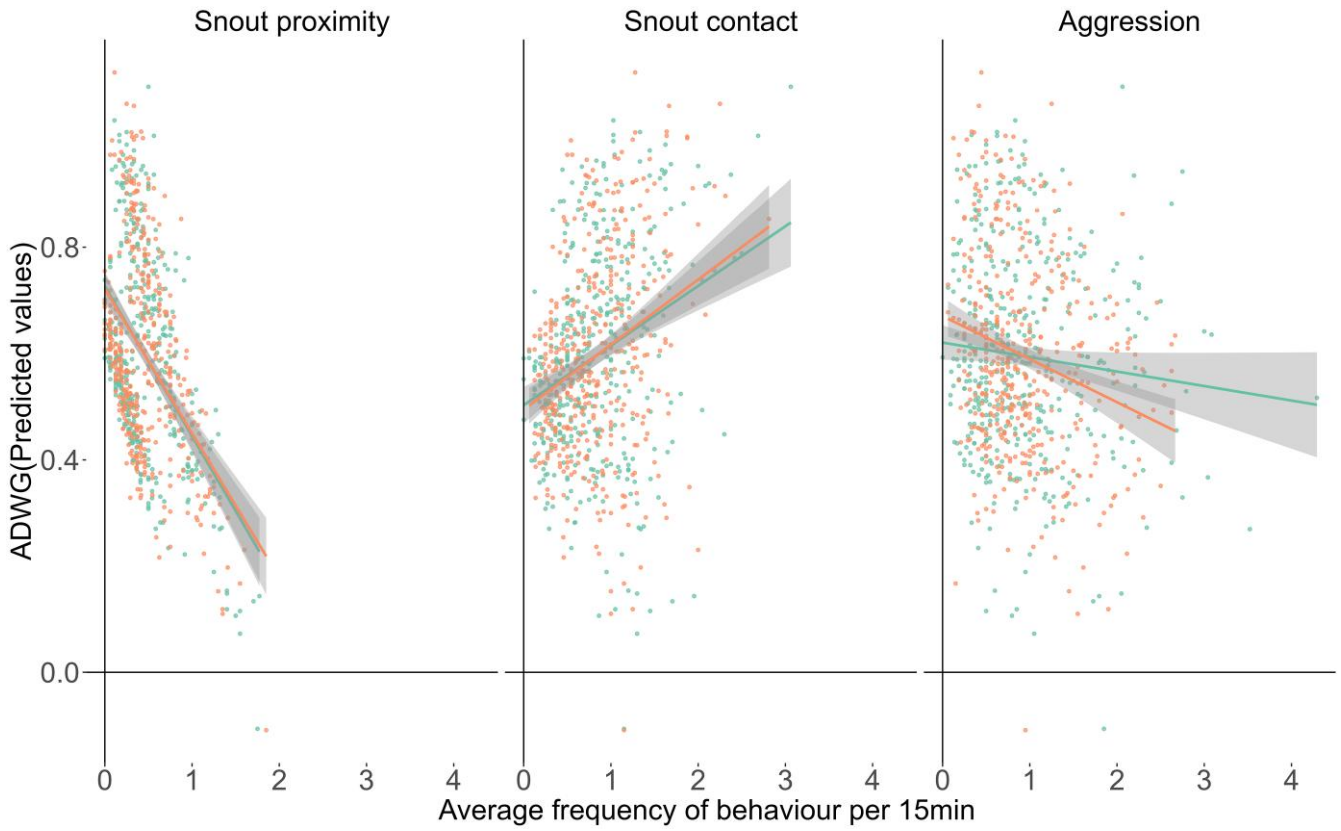


Figure 3. Relationship between the average daily weight gain (ADWG, in kg/day) and behavioral expression of snout proximity, snout contact, and aggressive behavior for initiators (teal) and recipients (orange) of the behavior. The *x* axis shows the average frequency of behavior per 15 min. Predicted values refer to the fitted response value from the model.

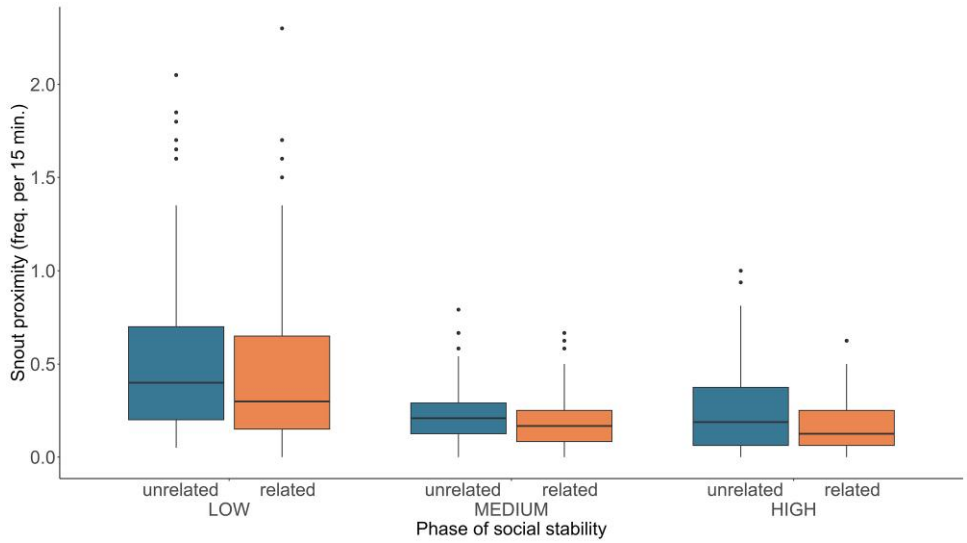


Figure 4. Frequency of snout proximity (per 15 min) directed towards unrelated pigs (nonlittermates; blue) and related pigs (littermates; orange) during the phases of low, medium, and high social stability.

through aggressive behavior and may escalate into a fight (e.g., Clark and D'Eath 2013; Camerlink et al. 2022). Individuals may therefore avoid direct contact upon encounter with unfamiliar conspecifics. While animals are primed to make optimal decisions (Bogacz 2007), the positive correlation between snout proximity and contact could suggest that the expression of nosing behavior does not relate to optimization of social information but rather conflict avoidance. Pigs that showed more snout proximity may have avoided conflict, and thus costs, but did have a lower growth performance. Rather than snout

proximity resulting in costs, such as energy expenditure and receipt of aggression (Vøllestad and Quinn 2003), it is more plausible that less well growing individuals, and thus weaker ones, will have had more reason to be risk aversive by showing more snout proximity. The benefits of nontactile over tactile behavior may depend on individuals' assessment of costs and benefits (Georgiev et al. 2013; Maestripieri 2021), and our results suggest that pigs adjust their behavior based on social context, which may especially be the case for the individuals who have a lower resource holding potential to engage in fights (Camerlink et al. 2022). Those individuals may trade-off the opportunity of tactile contact by choosing a lower risk of aggression by engaging in snout proximity instead.

The relationships between nosing behavior and growth could be due to a third confounding factor, such as dominance. Dominant pigs are typically (but not always) heavier and grow faster (e.g., Scheel et al. 1977) due to their preferential access to feed resources, which was not found in the current study. On the other hand, dominance is not the sole reason associated with weight gain (Meese and Ewbank 1973), and other factors such as high cortisol responses to stress (Hewagalamulage et al. 2016), sex differences, fearfulness (Page et al. 2019), or social stress (Tamashiro et al. 2007) can have an important effect. Dominant pigs showed more snout contact, but not more snout proximity. This may reflect dominant pigs' social ease in their higher ranked position, as they have less to fear from an aggressive response because the social hierarchy is maintained through active avoidance of dominant individuals by subordinates (Gonyou 2001). While the Modified David's Score (which was here based on overall aggressive encounters) is one of many standard approaches for observing dominance hierarchies, calculating the rank based on winners and losers of aggressive interactions might provide a more precise picture regarding the relationship between dominance, snout contact, and weight gain.

Behaviors expressed in dyadic interactions are affected by conditions such as familiarity (Patison et al. 2010; Kutsukake et al. 2019) and the physical and social environment (Rodenburg and Koene 2007), whereby dyadic interactions are formed based on individuals' ability to utilize personal and social information (Dall et al. 2005). Pigs use olfactory cues to distinguish familiar and unfamiliar conspecifics (Kristensen et al. 2001) and need to come in close proximity for olfactory recognition (Schild and Rørvang 2023). It is therefore reasonable that pigs that were unfamiliar to each other had more frequent snout proximity. However, the finding of more snout contact between unrelated pigs contradicts the theory that snout contact would be more associated with affiliative behavior (Camerlink and Turner 2013).

Males showed more snout proximity, but not contact, than females. This relates to previous work that shows that males show more ritualized agonistic behavior and take longer before engaging in contact, supposedly because the costs of escalated aggression between males are greater than between females (Camerlink et al. 2022). Pigs housed in enriched conditions exhibited less frequent snout proximity and contact than pigs in less-enriched conditions even when the space was adequately available. This is in line with the studies on behavioral differences between barren and enriched housing conditions, in which animals in enriched conditions perform fewer social interactions due to more frequent engagement with objects in the environment (e.g., Luo et al. 2020). Further, early life socialization did not influence snout contact or snout proximity. Early life socialization has been suggested to reduce pigs' aggressive behavior later in life (D'Eath 2005; Verdon et al. 2016) and to influence sociocognitive development (Weller et al. 2020), although it did not influence social play behavior (Weller et al. 2019).

Time, and thus the animals' age, presents a natural confound with social stability. However, social behavior remains largely unaffected by age in juvenile (O'Malley et al. 2022) and sub-adult pigs (Seddaiu et al. 2024) but it can fluctuate depending on the social context (O'Malley et al. 2022). For example, regrouping has a profound effect on the level of aggression (e.g., D'Eath et al. 2010; Turner et al. 2017). Indeed, in the current study, littermates showed a stable frequency of snout proximity and contact, aside from the low stability phase when they were regrouped with unfamiliar pigs. We can therefore be reasonably confident that the differences in behavior are related to the level of social stability rather than the change in age.

In conclusion, the positive association between snout contact and body weight gain, and the negative association between snout proximity and body weight gain suggests some behavioral trade-offs. Although the direction of the relationships would benefit from further study, the data suggest that in a situation of low social stability, slower growing individuals, who likely would suffer greater costs from escalated contact, may adapt by showing nontactile behavior to avoid direct physical contact, while snout contact has a relationship with enhanced growth performance. Hence, during group formation, snout proximity seems more related to conflict avoidance and conspecific recognition, whereas snout contact may have a more affiliative role in social interactions. These results add to the body of literature that shows that regrouping pigs into new social groups is detrimental for their welfare. It further emphasizes the relevance of observing nuances in animals' social behavior to gain a better understanding of how they adapt to adverse circumstances.

Acknowledgments

We would like to thank the animal technicians at SRUC for their help with the experiment.

Funding

The animal experiment was funded by the BBSRC (Biotechnology and Biological Sciences Research Council), grant number BB/V001515/1, and was conducted in collaboration with Queen's University Belfast and the Pig Improvement Company (PIC). SRUC receives support from the Scottish Government. The behavioral data collection and analysis for this study is part of a project funded by Narodowym Centrum Nauki Poland (NCN), grant number 2020/39/B/NZ8/02508.

Conflict of Interest Statement

The authors declare that they have no conflict of interest.

Ethics Statement

This noninvasive behavioral study adhered to the guidelines approved by SRUC's Animal Experiments Committee. The experiment was authorized by the UK Home Office (Project

Licence: PP1403242). The study was part of a larger overarching research project which imposed different housing conditions as treatments. These are accounted for in the statistical analyses but are not the focus of this study.

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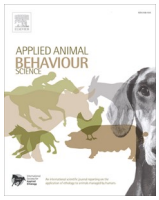
Applied Animal Behaviour Science 292 (2025) 106838

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim



Temporal social network structures based on snout contact during group integration in pigs

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ARTICLE INFO

Keywords:
Sus scrofa
Social nosing
Social network analysis
Group dynamics
Social behaviour
Aggression

ABSTRACT

During the formation of new social groups, temporal variations in behavioural associations between individuals can provide insight into the role of behaviours during group formation. While social behaviour during the establishment of new groups has been studied, there is a lack of knowledge on how non-agonistic social patterns change across time. The aim of this study was, therefore, to examine temporal variation in behavioural associations between individuals during the formation and maintenance of social relationships between conspecifics. This was studied in 15 mixed-sex groups of commercial pigs (n = 118 pigs; 8 pigs per group), which were regrouped at the start of the experiment (at weaning). They were studied between 4 and 11 weeks of age to capture variation in group stability. We focused exclusively on snout-directed behaviour given its role in conspecific recognition and affiliative interactions, whereby particularly snout-to-snout contact may contribute to the development of social relationships. Social network analysis (SNA) was used to investigate temporal associations. The results show that pigs made frequent snout contact (avg. 33 times / 15 min.) and that interactions were relatively more affiliative than aggressive (tenor range: 0.52 – 0.61), and were more affiliative in the high as compared to medium social stability phase (p = 0.02). As group integration progressed, the number of social partners involved in snout contact decreased, while the frequency of snout contact per individual increased. There was no evidence of non-random social preferences and no evidence of centralised associations (degree centralisation range: 0–0.3). Pigs showed more snout contact with non-littermates than littermates (i.e. a heterophilic association based on litter origin; assortativity range: −0.34 to −0.08) and between individuals with different early social experiences (assortativity range: −0.45 to −0.07) across all integration phases. Additionally, males initiated contact more frequently than females, whereas females occupied more central positions within the social network. These behavioural processes, which support the formation and maintenance of social relationships, show that non-agonistic behaviours such as snout contact have a prominent role in the social dynamics of pigs.

1. Introduction

Social relationships can influence the maintenance of group stability and are therefore important to consider in group-living animals (Stanley et al., 2018; Gomes et al., 2022). Individuals differ in the quantity and quality of relationships they maintain with social partners (Grueter et al., 2020) and may show preferences for whom they interact with. For example, animals can prefer to interact with group members based on traits such as age, sex (Carter et al., 2015; Perryman et al., 2019), dominance similarities (Gomes et al., 2022), and personality (Johnson et al., 2017). Social preferences have been shown in various farm animal species (e.g. cattle: Foris et al., 2021; pigs: Goumon et al., 2020) and are important to consider. However, social relationships are typically dynamic and subject to change, as group compositions may be disrupted by factors such as the arrival of new animals, the departure of existing group members, environmental factors or animals' age and experience, amongst other reasons. When social relationships are disrupted, individuals are forced to engage in new interactions to rebuild their social relationships (Nuñez et al., 2015; Lee et al., 2022), which is expected to result in differential interaction patterns (Sachser, 2005; Silk et al., 2013).

Pigs (*Sus scrofa*) form close social groups when allowed to do so

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https://doi.org/10.1016/j.applanim.2025.106838
Received 1 August 2025; Received in revised form 2 October 2025; Accepted 12 October 2025
Available online 13 October 2025

(Podgórski et al., 2014) and form preferential associations (Durrell et al., 2004; Goumon et al., 2020). In farm settings, social groups frequently change, especially after weaning, as pigs are regrouped with unfamiliar pigs to optimize farm management (Peden et al., 2018). When unfamiliar pigs meet, they need to establish new dominance relationships, which results in heightened aggression (Meese and Ewbank, 1973). During the first 24 h after regrouping, pigs remain close to those familiar to them while spacing away from others (Camerlink et al., 2014). It takes up to 48 h until a group has formed a new hierarchical structure (Meese and Ewbank, 1973) and up to 3 weeks to reach social stability (Stookey and Gonyou, 1994), while non-agonistic behaviours including social nosing may be altered for up to 9 weeks or more (O'Malley et al., 2022). Aggression at regrouping has been well documented (e.g. Schmolke et al., 2004; Turner et al., 2017; Büttner et al., 2020a) and has typically been the focus of research (e.g. O'Malley et al., 2022) due to its negative impact on animal welfare. However, the role of non-agonistic social interactions on the formation and of relationships during and after such regrouping events is much less explored.

In pigs, social nosing (i.e. social behaviour related to snout contact) has an important role in their social relationships (Petersen et al., 1989; Camerlink and Turner, 2013) and contributes to mother-offspring bonding (Blackshaw and Hagelsø, 1990), conspecific recognition, and affiliative interactions (Meynhardt, 1978; Kristensen et al., 2001). Moreover, the receipt of social nosing has been related to increased growth performance and may consequently have important implications for an individual's health and welfare (Camerlink et al., 2012). Recent work has shown that direct snout-to-snout contact differs from snout-to-snout proximity, whereby proximity is more generic and related to recognition whereas contact is more selective (Jowett et al., 2025).

We aimed to investigate the pattern of snout-to-snout contact behaviour (hereafter, snout contact) during group integration to better understand how non-agonistic behaviour influences the formation and maintenance of social relationships. We thereby considered the influence of factors such as familiarity, genetic relatedness and early life experience. Social Network Analysis (SNA) was used to investigate social dynamics at the individual and group level. We expect that, over time, group cohesion increases with a division of social roles and selectiveness based on relatedness. We further expect that, as social integration progresses, preferential associations start to form.

2. Materials and methods

This non-invasive behavioural study formed part of a wider experiment that received ethical approval by SRUC's Animal Experiments Committee and was authorised by the UK Home Office (Project Licence: PP1403242).

2.1. Animals and housing

A total of 118 domestic pigs (Large White × Landrace sows × American Hampshire boars) were studied at the Easter Howgate Pig Research Unit. Males (not castrated) (n = 59) and females (n = 59) from 15 litters were observed from four weeks of age to 11 weeks of age across three batches (i.e. cohorts). As part of an overarching experiment, approximately half of the litters underwent early-life socialization by allowing the piglets of two litters to mingle freely between two adjacent farrowing pens, while the sows remained within their pen (following Camerlink et al., 2018). Socialization was started when piglets were on average 12 days of age and continued until weaning, when all socialized pigs were relocated to their own farrowing pen with their biological mother. At weaning, socialized pigs were weighing on average 8.69 ± 0.96 kg (mean ± SD) and non-socialized pigs 9.15 ± 1.14 kg.

Pigs were weaned from the sow at four weeks of age and relocated to another research building. There, pigs were regrouped to form new social groups (8 pigs per group, balanced by sex). Each experimental group consisted of pigs from two litters that were unfamiliar to each other, with four siblings per litter. Litters that were previously socialized were not housed together, so that all new groups contained fully unfamiliar pigs. Groups were either housed in enriched conditions (average body weight in mean ± SD: 8.9 ± 1.12 kg) (ENR; n = 7 groups) or in less-enriched conditions (8.9 ± 1.06 kg), hereafter referred to as 'Control' (CON; n = 8 groups). ENR pens were 6.9 m × 2.1 m (14.5 m^2; 1.8 m^2 / pig) with deep straw bedding, Porcichew pig toys, and hessian ropes, while CON pens were 4.6 m × 2.1 m (9.7 m^2; 1.2 m^2 / pig) with rubber mats and wood shavings but no straw or toys. The ambient temperature in the building was monitored and heated to be within the thermal neutral zone for pigs. Pigs were fed *ad libitum* with commercial pig feed and had a continuous water supply via nipple drinkers. Pigs were ear-tagged and had a spray mark on their back with animal marker spray for identification, which was redone on the day before observations. Three individuals were removed from the groups due to health issues.

2.2. Behavioural observations

Snout contact and aggression were recorded using the "Animal Behaviour Pro" application (Newton-Fisher, 2021) installed on an iPad. Snout contact was defined as a pig touching the snout (area below the eyes, including the nose disc) of another pig with its nose disc. Aggressive behaviour was recorded when a pig delivered a head knock, threat, push or bite to another pig, or engaged in a mutual fight (a rapid sequence of biting). A bout of aggression could include moments in which the opponents stood still (pause) to regain breath and continue, until one retreated or until another behaviour (excluding standing still) was shown for at least 3 s.

Behavioural observations using continuous sampling were performed when pigs were 4–11 weeks of age (excluding week 9 due to farm management reasons). An observation session consisted of 15 min of continuous observation per group, while scoring all eight pigs simultaneously for the frequency of snout contact. Each group was observed for 3–4 sessions per day (between 07:00 and 17:00 h) in random order to avoid order effects, resulting in 45 min to 1 h of observation per group per day. In week 4, groups were observed for 3 days due to weaning, whereas in weeks 5–11 (excluding week 9), groups were observed for two days a week, resulting in approximately 15 h of observations per group. Live observations were done while standing at a distance from the pen to avoid disturbing the pigs. Due to farm management procedures at certain times of the day, which would disrupt live observations, part of the observations was scored from video. Groups were video recorded with two cameras per pen to capture the full area. Videos were available from 07:00–17:00 whereby periods with human disturbance were excluded from observation. For behaviours needing confirmation, videos were rewound by approximately 15 s. Overall, 33 % of the data were analysed from video, watched at regular play-back speed. All observations were conducted by a single observer.

2.3. Categorization for group integration

Pigs were regrouped at weaning, as described above, by mixing two litters to obtain groups of 8 pigs each (typically 4 pigs from each litter). The expectation from such a regrouping process was that young pigs would build social relationships between familiar and unfamiliar individuals, with variation in their association patterns as time progressed. Based on the durations that are described in the literature for the establishment of new dominance relationships, weeks 4 and 5 were categorised as low social stability (21.5 h of observation), weeks 6–8 as medium stability (21 h of observation), and weeks 10 and 11 as high social stability (16 h of observation) (Tong et al., 2019; Büttner et al., 2020a; Prevolnik Povše et al., 2021). These three phases of Low, Medium and High social stability were used to assess changes over time.

2.4. Tenor and social preferences

The nature of associations was assessed using the Tenor index as proposed by Silk et al. (2013). The tenor index shows whether the behaviours are mostly affiliative (value close to 1) or mostly hostile (value close to 0). The tenor was calculated, for each social stability phase, as the frequency of affiliative behaviour per observation period divided by the frequency of all affiliative and agonistic behaviour summed (following Fischer et al., 2017). Social preferences were assessed, for each social stability phase, based on the frequency of snout contact between individuals (method described in statistical analysis section).

2.5. Social network measures

Social network analysis helps to understand social associations at the individual and group level (Krause et al., 2007; Wey et al., 2008). In network theory (Wey et al., 2008), a social group with more than two members (also called actors or nodes) is connected via social relationships or interactions. These connections (referred to as edges) can be one-directional (unilateral) or bi-directional (reciprocal). The frequency of interactions provides weight to the relationships. Various individual and group network measures can be utilised to understand the variation in social associations (Pasquaretta et al., 2014; Sosa et al., 2021). In this study, we aimed to examine the temporal variation in the patterns of social interactions via the frequency of snout contact.

Based on previous studies (Makagon et al., 2012; Pasquaretta et al., 2014), we chose clustering coefficient, average local efficiency, degree centralisation, and modularity as the group-level network measures (Table 1). These measures describe whether (i) the network is centralised around one individual, (ii) the flow of social information occurs quickly through the group, (iii) the network has a high tendency, among the nodes, to form clusters indicating a high level of local interconnectedness, (iv) the network divides into communities with nodes in the same community densely connected, whereas sparse connections exist between different communities and (v) whether individuals direct snout contact behaviour towards individuals with similar traits.

At the individual level, we included measures of degree centrality, eigenvector centrality (Sosa et al., 2021), node level clustering and R-index (Liao et al., 2018) and node level clustering coefficient. These measures describe whether (i) the number of social partners and the frequency of association across the period of group integration changes during social integration, (ii) individuals' social positions change over time, (iii) the degree to which nodes in a network tend to cluster together forming a clique (a network of fully connected individuals), and (iv) individuals are more active in performing the role of initiator or recipient in social interactions.

We expect groups to have a community structure, whereby individuals from one litter will interact more with their siblings and gradually increase their interactions with non-littermates over time. This is expected to result in the disappearance of a community structure over time at the group level. At regrouping, pigs will need to establish new dominance relationships, and therefore, we expect the behaviour during the low social stability phase to be less centralised but to become more centralised over time.

2.6. Social Network Analyses (SNA)

SNA was performed using the library "igraph" (version 2.1.4) (Csárdi et al., 2025) in R (version 4.3.2) (R R Core Team, 2023). Behavioural data from 15 groups were included for the analysis. Out of 15 groups, two groups consisted of seven individuals (due to pigs being removed for health reasons), and the remaining groups had eight individuals. Normalised values adjusted for group size were used whenever the network measures accommodated normalisation. To assess whether the social networks differed based on the inclusion of video data, networks for live observation only and networks for live+video data were compared using Hamming distance. Hamming distances (a value from 0 to 1; whereby 0 denotes identical networks) for all three batches showed that the network structures remained mostly similar (batch 1, range: 0–0.14; batch 2, range: 0–0.01; batch 3, range: 0–0.02). Since Hamming distance only considers binary values (presence or absence of a connection between individuals), a correlation of degree centrality was performed between the live observation and live+video observation networks to confirm that the networks created from the inclusion of video observation data were not aberrant. A negligible correlation was observed in two groups (-0.08 – 0.07), a moderate correlation in another two groups (0.31 – 0.51), and a high correlation in 11 groups (0.79–0.98), suggesting that inclusion of video observations did not alter the structure of network compared to networks based on live observations. Hence, live

Table 1
Description of the chosen group- and individual-level social network properties.

Network measure	Purpose	Value range
Group level		
Degree centralization	Measures the extent to which snout contact is concentrated on a single or few individuals.	0 (decentralized network) to 1 (centralized network)
Average local efficiency (out-degree)	Indicates the spread of a behaviour as indicated by the average number of social partners it interacted with.	0–1 (efficient transmission of behaviour)
Clustering coefficient	Measures the cohesion between individuals in a group, as indicated by the proportion of fully connected triads in the group.	0 (no cohesion) to 1 (cohesion)
Modularity	Measures the fragmentation of a group.	0 (random relationships) to 1 (strong hierarchical clustering)
Assortativity	Determines the tendency of nodes to connect to other nodes that are similar in some attributes.	−1 (nodes tend to connect to nodes with different attributes) to 1 (same attributes between nodes)
Individual level		
R-index (social role)	Measures individuals' inclination towards a social role (initiator or recipient). $RI_i = wo_i/(wi_i + wo_i)$, where RI_i is the R-index of individual i, wo_i is the weighted outdegree, and wi_i is the weighted indegree. In- and out-degree indicates the number of social partners an individual received contact from (in-degree) or initiated contact with (out-degree), weighted by frequency.	> 0.5: an individual undertakes the role of initiator
Degree centrality: unweighted out-degree	Unweighted centrality: as above (for group-level), weighted by frequency of contacts initiated towards social partners.	0 (no social partner) to 6 or 7 (max. number of social partners per individual, in this study)
Degree centrality: weighted out-degree	Weighted centrality: to measure the variation in the amount of association as the group integrates	0 (infrequent contact) to max frequency of contact
Eigenvector centrality (social position)	Measures the social position of a node based on the connections of the node to whom the focal node is connected in a social group.	0–1; the higher the more individuals connected to well-connected individuals.
Node clustering coefficient	Measures a node's neighbours' inclination to form a complete clique (a fully connected subgraph).	0 (no cohesion between neighbours of a node) to 1 (max. cohesion)

and video data were combined.

The five group-level measures for the social network – degree centralisation, average out-degree local efficiency, global clustering coefficient, modularity, and assortativity – were calculated in R using the library "igraph" (Csárdi et al., 2025). The five individual-level measures – degree centrality (unweighted and weighted), eigenvector centrality and R-index were calculated using the igraph library and, node clustering coefficient using the "DirectedClustering" package (version 0.1.1) (Clemente and Grassi, 2018), in R (see supplementary material for R script).

2.7. Statistical analyses

2.7.1. Analysis of social network metrics

The social network measures were subsequently analysed to assess differences between the social stability phases and which factors may influence the metrics. The differences in the network metrics at group level across phases of integration were tested using a paired Wilcoxon signed rank test. Individual-level measures were built into mixed models as response variables to assess the effect of different predictor variables. Two types of mixed models in R (generalised linear mixed models with binomial distribution and beta distribution) were used. For each model, the best-fitting model was selected based on the lowest Akaike Information Criterion (AIC) value (Akaike, 1973). For all the models, the fixed variables were early-life socialisation treatment (socialised or non-socialised), housing condition (ENR or CON), sex (male or female), and social stability (low, medium, high). Batch and individual ID (nested within the group), were included as random factors.

Firstly, we performed a generalised mixed model with binomial distribution using the "glmer" function in the "lme4" package (Bates et al., 2015) (version 1.1–35.1). Individual-level social network measures of degree centrality (unweighted and weighted out-degree centrality) and R-index (for initiation of the behaviour) were response variables in three separate models. In the model with the unweighted degree centrality as the response variable, the specific binomial structure was defined as the number of unique social partners based on the theoretical maximum possible number of social partners. In the model with weighted degree centrality as the response variable, the structure was defined as the frequency of social associations for each social partner based on the maximum number of social associations. Similarly, the individuals' social role (R-index, whereby ratios $\geq$0.5 indicates the animal as an initiator) as response variable was included in another binomial mixed model.

A model with a beta distribution was built for the proportional response variable of eigenvector centrality (where higher values denote that individuals occupy a more central position in the group interacting with well-connected partners). Since eigenvector centrality values are in the range from zero to 1, the value of zero was changed to "0.0001" and "1" into "0.9999" to accommodate the mixed model using glmmTMB (Brooks et al., 2017) (version 1.1.9) in R. Similarly, individuals' local clustering coefficient based on weights (frequency of association) was modelled using a beta distribution. Post-hoc tests were performed using the "emmeans" package (version:1.8.9) (Lenth, 2023).

2.7.2. Analysis of tenor and social preferences

For the tenor, the normality and variance were tested using the Shapiro-Wilk test and Levene's test. A repeated measures anova was performed, followed by a post-hoc paired *t*-test with Bonferroni correction to test the differences between the social stability phases.

The strength of social associations among pairs of individuals was based on the frequency of snout contact and analysed via a Monte Carlo permutation test. Association matrices based on snout contact were constructed for each group (15 groups) across 3 social stability phases, resulting in 45 association matrices. The permutation test was performed using the library "ade4" (Dray and Dufour, 2007) (version 1.7–22) and "vegan" (Oksanen et al., 2024) (version 2.6–8) to analyse if snout contact was directed towards preferred social partners significantly more than by chance. When the observed coefficient of variation (CV) was greater than the random matrix in more than 95 % of the permutations ($p < 0.05$), the variability in the preferential association matrix was considered non-random and significant (Patriquin et al., 2010; Manly, 2018). A total of 1000 random permutations were generated from observed association matrices, by allowing the total number of individuals and the number of associations from the observed matrix to be the same (Bejder et al., 1998; Whitehead et al., 2005) and the p-value based on permutation was calculated.

Additionally, the influence of litter origin and early life socialization was calculated using the Mantel permutation test on the half-weight index (HWI) (Cairns and Schwager, 1987). The Mantel test measures whether the pattern of differences (or similarities) between pairs of items in one matrix is correlated with the pattern in another matrix (Legendre, Fortin and Borcard, 2015). The HWI was calculated as $X/(X + Y_{ab}+0.5(Y_a+Y_b))$, where X is the frequency in which "individual a" and "individual b" were reciprocally interacting, Y_{ab} is number of times both individual "a" and "b" are located separately in different groups, Y_a is the number of times "individual a" initiated interaction with "individual b" but not "individual b" with "individual a" (i.e. a's interaction was not reciprocated), and Y_b is the number of times "individual b" initiated interaction with "individual a" but not "individual a" with "individual b". As the observations were performed in a closed system (no change in group composition after regrouping), individuals could not be located separately in different groups. Hence, the term "Y_{ab}" in the HWI equals zero, and the HWI calculation changes to, $X/(X + 0.5(Y_a+Y_b))$, similar to the modification performed in previous studies (Lusseau et al., 2003). After considering the HWI, a dissimilarity matrix based on two social stability phase comparisons (e.g., low-mid) for each dyad, including a distance matrix based on the grouping variable (litter origin, socialisation), was constructed. The HWI was calculated to quantify the strength of the associations between individuals across time (low-medium and medium-high social stability), and a Mantel test was performed to estimate how the association was affected by traits of the individuals such as relatedness and early life socialization. The Mantel test with 1000 permutations was performed to examine the association depending on individuals' litter origin, using the "dist" function from the "vegan" package (Oksanen et al., 2024).

3. Results

3.1. Temporal variation in group-level network properties

Across 15 groups (118 pigs), a total of 7521 snout contacts were recorded based on 56.5 h of observation (mean interactions per group 501.4; SE = 4.18). Overall, there was little variation in the network measures across the integration phases (Table 2). However, differences were found in certain network measures at the group level between the

Table 2
Median and minimum and maximum value (in brackets) of group-level social network metrics for networks based on snout contact, in 15 groups of ~8 pigs during low, medium, and high social stability.

	Low stability	Medium stability	High stability
Modularity	0 (0 – 0)	0 (0 – 0.02)	0 (0 – 0.10)
Degree centralisation	0.06 (0 – 0.22)[a]	0.12 (0.02 – 0.30)[ab]	0.14 (0.02 – 0.30)[b]
Average local efficiency (out-degree)	0.41 (0.17–0.67)[a]	0.49 (0.26 – 0.68)[b]	0.44 (0.22 – 0.71)[ab]
Clustering coefficient	1 (0.64 – 1)	0.98 (0.74 – 1)	0.96 (0.52 – 1)
Assortativity	−0.12(−0.14–	−0.16(−0.34 –	−0.16(−0.20 –
Socialisation	−0.08)[a]	−0.12)[b]	−0.09)[ab]
Litter origin	−0.12(−0.31–	−0.15(−0.45 –	−0.15(−0.27 –
	−0.04)[a]	−0.08)[b]	−0.07)[ab]

[ab] Values that lack a common superscript indicate a significant difference.

low and medium social stability phase. Specifically, average local efficiency increased in the medium stability phase (paired Wilcoxon signed-rank test, V = 17, n = 15, p = 0.01) and degree centralisation differed between the low and high social stability phase, whereby degree centralisation increased in the high stability phase (V = 94, n = 15, p = 0.01).

The network measures (Table 2) indicate an absence of a clear community structure (as indicated by modularity) and shows a high connectivity between the neighbours of nodes (as indicated by the clustering coefficient). Additionally, snout contact appeared to spread only moderately from one node to others (via dyadic efficiency), implying that when an individual engaged in snout contact, this did not encourage others to do the same, and thus, not all individuals engaged equally in snout contact. The network based on snout contact was relatively decentralised (as shown by degree centralisation), indicating that behaviour was not disproportionately performed or received by a small number of individuals. Furthermore, assortativity values indicated that nodes tended to connect with dissimilar individuals (thus showing heterophily) in terms of socialisation treatment and litter origin, indicating that socialised pigs associated more with non-socialised ones (and vice versa) (V = 28, n = 8, p = 0.02) and that individuals from different litters engaged more in snout contact with each other than with litter mates (V = 28, n = 15, p = 0.02).

3.2. Temporal variation in individual-level network properties

The likelihood of individuals forming unique social associations through snout contact decreased as group integration progressed (measured by unweighted degree centrality) (Table 3). While there was no significant difference in this likelihood between the medium and high social stability phases, a difference was observed between the low and medium phase, as well as between the low and high social stability phases for unweighted degree centrality. The frequency of associations, measured by weighted degree centrality which reflects the strength of social ties, declined over time. In the high social stability phase, individuals exhibited less frequent snout contact as observed in the weighted social network (Table 3). Taken together with the reduction in unweighted degree centrality over time, this suggests a shift from broad social exploration with many partners, to more focused, repeated interactions with fewer social partners. The eigenvector centrality remained high throughout the observations, resulting in no significant differences between the phases (Table 3). Additionally, individuals' likelihood of connecting with other individuals, based on the node clustering coefficient, was higher during the low than the high social stability phase whereas a tendency (p = 0.06) for a higher likelihood of nodal clustering was observed in the low as compared to medium stability phase.

3.3. Factors affecting individual-level network structure and individuals' social roles

Males were nearly two times more likely to assume the social role of initiator compared to females (OR 1.92, $p = 0.007$, CI [1.188–3.116]). However, females were 1.5 times more likely to occupy more central social positions, reflected by a higher eigenvector centrality (OR 1.5, $p = 0.007$, CI [1.11–2.02]). Pigs housed in less-enriched environments were more likely to form a greater number of social relationships than pigs in the enriched housing condition (non-weighted out-degree OR 1.79, $p = 0.004$, CI [1.19–2.67]). Additionally, individuals in less-enriched conditions were more likely to form clusters within the network (clustering coefficient OR 1.98, $p = 0.031$, CI [1.06–3.69]). However, the housing conditions did not influence pigs' social position (eigenvector centrality) within the network. Similarly, early life socialisation did not significantly predict either the number of social partners or the social position or the clustering coefficient.

3.4. Tenor and social preferences

The nature of social relationships, measured using the tenor, indicated that interactions were predominantly affiliative across all three phases (low social stability: 0.59 ± 0.018, medium: 0.52 ± 0.019, and high: 0.61 ± 0.024; Fig. 2). The tenor differed between the medium and high social stability phase (p = 0.02) and tended to differ between the low and medium social stability phase (p = 0.06) (Fig. 2).

The Monte Carlo simulation did not reveal significant preferred associations between social partners based on snout contact, across any phase of social stability. Although the observed coefficients of variation (CVs) for snout contact were often higher than the mean random CVs, none of the observed CVs exceeded the 97.5th percentile of the random distribution. This indicates that the observed patterns were not significantly different from what would be expected by chance. Specifically, in none of the groups or phases did the observed CV fall outside the 95 % confidence interval of the randomised CVs, as reflected by p-values all above 0.05. While 10 groups showed observed CVs greater than the random CVs across all three phases, and 5 groups showed this pattern in one or two phases, these differences were not statistically significant. Therefore, the results suggest that there was no evidence for consistent or structured preferential associations based on snout contact during any of the phases. Further, there was no evidence of temporal stability (based on the Half Weight Index permuted 1000 times) across the phases of social stability due to traits such as relatedness (litter origin: n = 15 groups, Mantel test p > 0.05) and early life socialisation (n = 8 groups, Mantel test p > 0.05).

4. Discussion

Regrouping of pigs into new social groups, which is known to result in a re-establishment of dominance relationships to obtain social stability, impacted several group-level network measures in social networks based on snout contact. However, these changes were not substantial enough to fundamentally alter the overall structure of the social network. Social network analysis based on the frequency of snout contact throughout the social integration period revealed that, at the group level, interactions were: (i) random, lacking a strong hierarchical structure; (ii) decentralised, with snout contact not concentrated around a few individuals; (iii) moderately outward-directed, suggesting that all conspecifics were motivated to associate with social partners or acquire social information; (iv) indirectly connecting or bridging across all

Table 3
Network metrics (model-estimated probabilities) from individual-level networks and Odds Ratio (OR) from the best fitting model, based on 118 pigs across 15 groups. Values are emmeans with standard error (SE) based on the frequency of snout contact during low, medium and high social stability.

Means ± SE				Post-hoc OR		
Network measure	**Low**	**Medium**	**High**	**Low-Mid**	**Low-High**	**Mid-High**
Unweighted degree centrality (out-degree)	0.91 ± 0.044	0.86 ± 0.064	0.84 ± 0.070	1.64*	1.84*	1.12
Weighted degree centrality (out-degree)	0.64 ± 0.020	0.66 ± 0.020	0.58 ± 0.021	0.91	1.2*	1.4*
Eigenvector centrality	0.74 ± 0.022	0.71 ± 0.023	0.71 ± 0.023	1.13	1.14	1.01
Node clustering coefficient	0.82 ± 0.061	0.76 ± 0.074	0.71 ± 0.085	1.40	1.86*	1.34

* indicates values with P < 0.001.

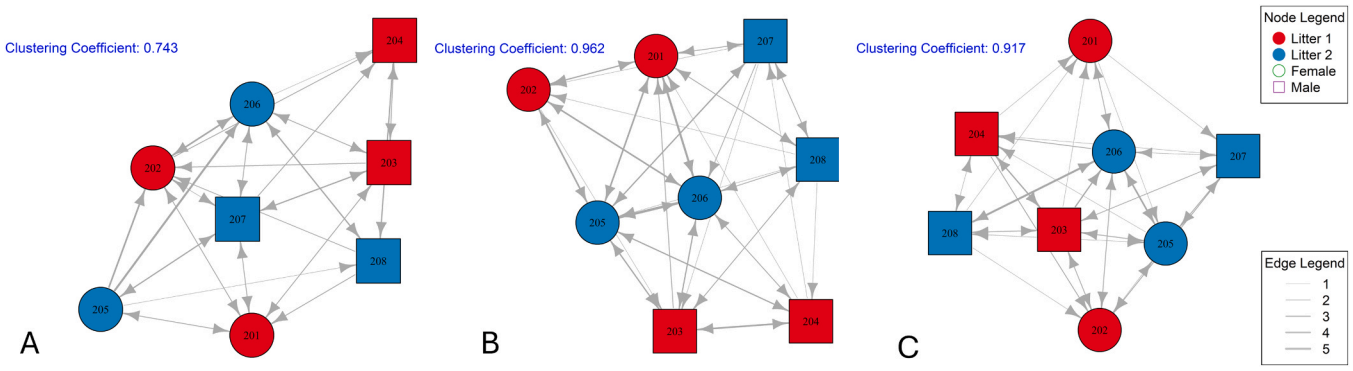

Fig. 1. Example of one group analysed with Social Network Analysis based on weighted and directed snout contact (shown by an arrow from the initiator to the recipient), by litter origin and sex for clustering coefficient during the different phases: A) low, B) medium, and C) high social stability. The node label includes the subject id. The thickness of edge legend reflects the frequency of snout contact.

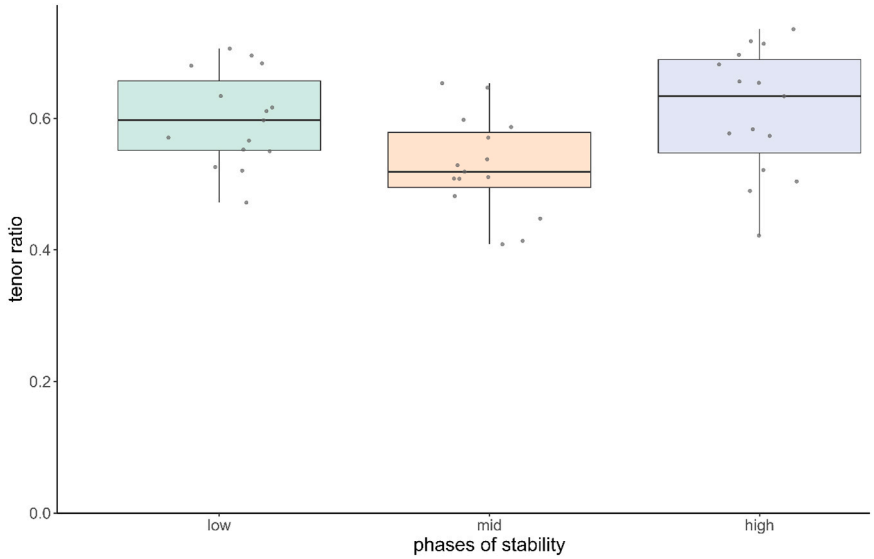

Fig. 2. A boxplot showing mean values for the tenor ratio (0 meaning more hostile interactions, 1 meaning more affiliative interactions) by phase of social stability (the medium stability phase differs from the high stability phase by $p = 0.02$).

social partners; and (v) heterophilic, i.e. occurring more between individuals who were from a different litter and had a different early life experience. Based on individual-level associations, we found that pigs reduced their number of social partners (as measured by degree centrality) as group integration progressed. Although the number of unique partners decreased, the frequency of social encounters (via weighted degree centrality) increased in the later stages, indicating more frequent snout contact. However, we found no evidence of strong or consistent partner preferences during any of the phases.

Snout contact is a predominant behaviour between domestic pigs, regardless of age (Portele et al., 2019; Seddaiu et al., 2024). It was expected that snout contact would be frequent during regrouping (Jowett et al., 2025), but particularly when social stability increases due to its affiliative nature. We indeed found that snout contact was frequent between group mates (ca 33 times per 15 min). As group stability increased, snout contact was shown more frequently but to fewer individuals. The clustering coefficient indicated strong social circles based on snout contact during the early phase of group integration, suggesting that pigs interacted with all group mates, which subsequently diminished (though not substantially) as group integration progressed. The reduction in social partners, even in the small group of eight pigs in this study, suggests that pigs, like other social animals, could prioritize acquisition and transfer of information, where individuals are selective in building relationships (Blumstein et al., 2004). In commercial farms, social groups are likely to be larger, which may influence network dynamics such as clique formation (e.g. Foister et al., 2018; Büttner et al., 2020b).

The social network analysis revealed different social roles for males and females. This study included groups that were balanced for sex, including both females and entire males in each group. Males were more likely to initiate snout contact, suggesting that young males are more proactive in seeking social contact, thus increasing their frequency of social encounters. This relates to a previous study where entire male pigs expressed more social interactions (nosing behaviour and agonistic behaviour) (Clouard et al., 2022). In nature, young males disperse from the family group to become solitary, only seeking a herd during the mating season, and therefore are inherently under different social pressures than females (Podgórski et al., 2014). While the males were only 4 weeks of age during the first observations, and therefore before puberty or their natural dispersal age, previous studies have also shown that, even at a young age, male pigs differ in their social behaviour from females (Brown et al., 2015; Fleming and Dilger, 2017). Having single-sex groups or a more ecologically relevant male:female ratio may change social associations (Tanida et al., 1992; Bieber et al., 2019). In contrast to the males, the females in this study showed a high likelihood of maintaining a more central social position (via eigenvector centrality)

in snout contact networks. Females live in sister groups (Podgórski et al., 2014) and may therefore be better equipped to maintain good social connections. Research from other species, including humans, suggests various pathways in which sexual dimorphism for social behaviour may be present and regulate social behaviour (e.g. Dumais and Veenema, 2016; Yang and Shah, 2016). Females may maintain social positions by connecting with well-connected individuals in the group, which helps in acquiring benefits from affiliative interactions as evidenced by eigenvector centrality. Attaining a social position by connecting with individuals who are more important in the network can help in the gathering of reliable social information and performance of affiliative interactions, and to reduce aggression (Hasenjager and Dugatkin, 2015; Canteloup et al., 2021) or social stress. For example, adult sows who were more socially prominent (based on higher levels of body contact during resting) were inclined to have fewer stillborn piglets than less socially prominent sows (Jowett et al., 2024). Understanding the influence of pigs' social positions (via eigenvector centrality) on later life fertility could provide more insight into the biological relevance of males' and females' approaches to selecting different strategies for forming social relationships. Overall, the sex differences, whereby males initiate frequent snout contact and females are more likely to attain a higher social position, indicate that a socio-biological demand might have contributed to such variation between individuals.

In the more enriched housing conditions, pigs showed a lower likelihood of forming connections with all group members via snout contact, as compared to less enriched housing conditions. A main difference between these two housing conditions was the presence of deep straw bedding in the more enriched conditions. Straw is known to be highly attractive to pigs (Fraser et al., 1991), and they invest a considerable amount of their time budget in straw-directed behaviour (Jensen et al., 2015). This is likely the reason why pigs in straw-based systems showed fewer social interactions than pigs from barren pens (Beattie et al., 2000; Averós et al., 2010; Mkwanazi et al., 2019). Although we did not observe pen-directed behaviour, we expect that the difference between the housing conditions is because of the interactions with bedding material rather than with penmates. From a welfare perspective, the presence of straw but reduced social contact is more in line with pigs' natural behaviour as in a semi-natural environment they spent large amounts of time on exploration and little time on social interactions (Stolba and Wood-Gush, 1989). Additionally, the floor space allowance was smaller in the less enriched pens, which may have increased the proximity and likelihood of contact between pigs. The less enriched conditions, which served as a control treatment to reflect commercial farm conditions, are considered to be poorer from an animal welfare perspective. Yet, the increased snout contact interactions could have beneficial effects on pigs' growth performance (Khatiwada et al., 2025) and therefore may provide a social benefit in spite of the suboptimal environmental conditions.

We found that the nature of social associations among pigs was predominantly affiliative rather than aggressive, which may partly be because half of the group already knew each other from birth. However, we did not find evidence of statistically significant social preferences within the groups based on snout contact. In a previous study on pigs of similar age, no social preferences were found based on snout contact, but social preferences were present when calculated based on lying in contact (Clouard et al., 2024). Snout-related behaviour (also referred to as social nosing) serves multiple purposes (Camerlink and Turner, 2013), whereby tactile contact is seen as more affiliative (Goumon et al., 2020). However, as associations based on spatial proximity may be influenced by environmental factors (Camerlink et al., 2022) and preferences for lying locations (Durrell et al., 2004), it is yet unclear whether such associations truly reflect affiliative preferences (Goumon et al., 2025). Therefore, while it has been suggested that snout contact is a better measure of affiliative behaviour than lying behaviour (Seddaiu et al., 2024) and thus preferred for calculating social relationships (Goumon et al., 2025), it is still unclear whether social preferences based on snout contact are truly present. For now, the absence of social preferences for snout contact, during any phase of social stability, suggests that young pigs are not socially selective when expressing snout contact.

Funding

The animal experiment was funded by the BBSRC (Biotechnology and Biological Sciences Research Council), grant number BB/V001515/1, and was conducted in collaboration with Queen's University Belfast and the Pig Improvement Company (PIC). SRUC receives support from the Scottish Government. The data collection reported here is part of a project funded by the National Science Centre (NCN), Poland, grant number 2020/39/B/NZ8/02508.

CRediT authorship contribution statement

Sunil Khatiwada: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Victoria E. Lee:** Writing – review & editing, Project administration, Investigation. **Irene Camerlink:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Simon P. Turner:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

Given her role as Editor-in-Chief, Irene Camerlink had no involvement in the peer review of this article and had no access to information regarding its peer review. Full responsibility for the editorial process for this article was delegated to another journal editor.

Acknowledgements

We would like to thank the Lucy Oldham and animal technicians at SRUC for their help with the experiment.

Appendix A. Supporting information

Supplementary file (R script) associated with this article can be found in the online version at doi:10.1016/j.applanim.2025.106838.

Data availability

The data used for analysis in this study is available at DOI: 10.17632/txtj2khy35.1

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Behavioural Processes 222 (2024) 105099

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Leadership amongst pigs when faced with a novel situation

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ARTICLE INFO

Keywords:
Followers
Human approach test
Leader
Personality
Social behaviour
Sus scrofa

ABSTRACT

Leadership is a risky behaviour that can impact individuals and groups. Leaders, i.e. individuals who perform or initiate a task while other individuals in the group follow, have been studied in different contexts, but there is still a lack of understanding on the role of individual characteristics that may predispose them to become leaders, such as dominance and personality. In particular, the characteristics of leaders in domestic animal populations has been poorly examined. We studied leadership within 32 groups of young pigs (*Sus scrofa domesticus*, n = 366 individuals). Leadership was assessed during a group-based fear test (Human Approach Test) which was repeated three times. The first individual per group to touch the person was identified as leader. We assessed repeatability of leadership and characteristics of leaders as compared to followers. Leadership was marginally repeatable, with 6 out of 26 groups having a consistent single leader across all tests. Females had odds 4.13 times greater than males of being a leader, while there was no effect of body weight (a proxy of dominance) or coping style on leadership. The results indicate a similarity with wild populations, in which females lead the herd even though the males, which are superior in body weight, are often dominant.

1. Introduction

Individuals in a social group show various behavioural characteristics related to social life, such as leadership, dominance, boldness and sociability. Among these behavioural characteristics leadership is characterized as an individual's tendency to initiate movement at the front position (e.g., during a long journey), or to be the first to depart to perform a task or to recruit a partner (Fischhoff et al., 2007; King et al., 2008; Peterson et al., 2002). Mammalian literature, for example in horses, indicates that a single individual in a social group (wild or domesticated) eventually occupies a leadership position over time (Bourjade et al., 2015). The characteristics of leaders has been poorly studied in domesticated managed populations. In wild populations, leadership is a trait expressed by a highly motivated, dominant, and knowledgeable individual (King et al., 2009), often with a particular set of morphological, physiological, or behavioural traits (Boinski and Garber, 2000). Although studies have linked leadership expression with different individual attributes and other behavioural correlates (Boinski and Garber, 2000), the relationship between leadership and coping style (i.e. responses to stressful scenarios) has rarely been examined. An individual's coping style can have implications for health (Ruis et al., 2001; Korte et al., 2005) and fitness (Koolhaas, 2008), and therefore coping behaviours may be an important factor in the development of leadership.

Leadership traits in non-domesticated populations are linked with behavioural expression in other domains. For example, Kurvers et al. (2009) indicated, in barnacle geese (*Branta leucopsis*), a correlation between leadership traits and individual animal personality. Similarly, in zebra finches (*Taeniopygia guttata)* more active and explorative individuals arrived early at a food patch (Beauchamp, 2000; Schuett and Dall, 2009) and, in sticklebacks (*Gasterosteus aculeatus*), bolder individuals displayed more willingness to leave cover, both indicating a trait of leaders (Harcourt et al., 2009). Additionally, bolder pigeons (*Columba livia*), occupied higher ranks in the hierarchy and influenced the collective movement of flocks (Sasaki et al., 2018). Further, exploratory or bolder individuals undertook the leadership role by initiating searching for food instead of depending on other individuals (barnacle geese: Kurvers et al., 2012). Studies from sticklebacks also indicate that within a pair an individual can be a leader in one situation while being a follower in another context (Harcourt et al., 2009; Webster and Ward, 2011). The literature suggests that individual experiences and socio-ecological factors are important in shaping many domains of behavioural expression including leadership traits.

Leadership has been mostly studied in natural settings, typically

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https://doi.org/10.1016/j.beproc.2024.105099
Received 24 April 2024; Received in revised form 26 July 2024; Accepted 9 September 2024
Available online 10 September 2024

considering one or a few groups per site (King et al., 2009). This results in limited observations on the characteristics of leaders. Researching leadership in domesticated animals has the benefit that groups can be artificially formed, and henceforth many similarly composed groups can be studied for their leadership dynamics. The process of domestication and the provision of abundant resources in managed domesticated populations may have negated the benefits of leadership and relaxed selection pressure for leadership or even resulted in artificial selection against leadership. Additionally, the characteristics shown by leaders may have changed. Leadership traits in domesticated animal groups have been reported, although sparingly (ewes: Addison and Simmel, 1980; cattle: Dumont et al., 2005; Valenchon et al., 2022). For example, cattle (*Bos taurus)* show leadership characteristics in decision making, such as searching newer feeding sites (Dumont et al., 2005; Šárová et al., 2010). In domestic pigs (*Sus scrofa domesticus*), leadership was suggested as early as 1973 (Meese and Ewbank, 1973a) but has not been taken further. Pigs do form dominance hierarchies (Meese and Ewbank, 1973b) and while dominance rank has indicated individual leadership, (cattle: Šárová et al., 2010; dogs (*Canis familiaris)*Ákos et al., 2014; bonobos (*Pan paniscus)*: Tokuyama and Furuichi, 2017) it cannot be generalised to all animal social structures.

The aim of this study was to investigate factors related to leadership traits in a domesticated population. This was studied in 32 groups of domestic pigs by assessing how coping style, sex and body weight influence leadership in a group-based novelty situation. Based on the existing literature, we expected that proactive and heavier individuals would have a greater likelihood of adopting a leadership role, as such individuals would theoretically suffer less from taking a risky behavioural strategy in some contexts (Wolf et al., 2007).

2. Material and methods

2.1. Statement of ethical review

This study followed the European Guidelines for accommodation and care of animals and was in accordance with the UK Government DEFRA animal welfare codes and adhered to the ASAB/ABS guidelines. The SRUC's Animal Ethics Committee and the UK Government Home Office (Project licence PPL60/4330) approved the experimental protocol (no. ED AE 21–2014).

2.2. Animals and housing

Male (n=184) and female (n=182) domestic pigs ((Large White × Landrace) × American Hampshire), originating from 53 litters, were studied across four batches (i.e., cohorts of litters born at approximately the same time). Piglets were raised in farrowing pens with the sow housed in a farrowing crate. At birth, they were weighed, vaccinated and identified with ear tags. Tails and teeth were kept intact and males were not castrated. Piglets were weaned from the sow at ~28 days of age and remained for one more week in the farrowing pen. The average weaning weight in males was 7.98 ± 1.41 kg (mean ± SD, range 3.7–12 kg) and in females 7.66 ± 1.48 kg (3–11.4 kg). Pigs had a positive daily body weight gain between week 2 and 4 of age (mean ± SD: 0.25 ± 0.07 kg / day, range: 0.05 – 0.48 kg / day) and between week 4 and 9 of age (mean ± SD: 0.46 ± 0.07 kg / day, range: 0.23–0.63 kg / day). Further, the proportion in body weight gain from week 2 to week 4 (range: 0.5 – 0.9, SD = 0.07) and week 4 to week 9 (range: 0.16 – 0.38, SD = 0.03) suggests that most pigs were following a similar growth trajectory between weeks.

At 5 weeks of age, they were moved to the research building, where they were kept within the same litter (no change in group composition). Group size was on average 12 ± 2 pigs. Pens had a solid floor with deep litter straw bedding and measured 1.9 m × 5.8 m (11 m^2), equating to 1.0–1.1 m^2 per animal. In winter, there was a covered kennel area made from straw. Each pen had a single-space feeder and a drinker, with *ad libitum* standard commercial pelleted feed and water. Lights were on from 07:00 – 19:00 and the room had natural daylight from ceiling height windows.

2.3. Backtest

The backtest is a commonly used behavioural test in piglets in order to assess their coping style (e.g., Zebunke et al., 2017). In total 366 piglets were tested in the backtest, as a reflection of coping style, following the procedure of Hessing et al. (1993) and as described by Melotti et al. (2011). Piglets were tested at 14 days of age (15.37 ± 1.02; range 13 – 18 days of age). The complete litter of piglets was taken to a room adjacent to the test room before the start of the experiment. The test order was balanced between litters of primiparous and multiparous sows (n = 14 and 20, respectively). For the test, the experimenter lifted at random one piglet out of the trolley and brought it to the test room. The experimenter placed the piglet in a supine position on a 25 kg feed bag which was located on a table, with a slight indent in the longitudinal direction (to support the piglet's spine). The piglet was held in this position for one minute. The experimenter placed one hand firmly on the piglet's thorax, with one of the piglet forelegs between thumb and index finger and the other foreleg between index and middle finger. The experimenter's other hand was placed loosely on the hind legs (Bolhuis et al., 2003). The handler counted the number of times a piglet resisted the experimenter's grip by struggling (i.e., escape attempts). One struggle was counted as movement of the body or legs by muscle tension, and lasted until the piglet relaxed the hind legs for at least a second. Another person counted the number of vocalizations. Each breath with a raised sound was counted as one vocalization. After the test the piglet was weighed and returned to the sow. Frequent vocalizations and struggles have been interpreted as a more proactive coping style (Spake et al., 2012), whereas during a reactive coping response piglets typically stay immobile and do not vocalize. The number of vocalizations ranged from 0 – 64 (median 8), and the number of struggles from 0 – 8 (median 1), showing sufficient variation in these traits for analysis. The distribution of these variables was skewed, with 24 % (n = 95) of pigs not vocalizing at all and 29 % (n = 114) not struggling.

2.4. Human approach test (HAT)

The HAT has been used to assess pigs' response to humans, especially fear of humans (Leliveld et al., 2017; Desire et al., 2023). In total, 366 pigs were tested at 6 weeks of age, when they had limited contact with humans besides routine farm care and the backtest. Three tests were carried out, once each during three afternoons (Thursday, Friday and Monday) in the same 7-day period, with the test order balanced between the groups. Pigs were marked on their back with animal marker spray for recognition, which was done the day or morning prior to the test.

One person, hereafter the 'experimenter', conducted all tests. The experimenter was not familiar to the pigs prior to the test and wore a red overall in order to differ in clothing from the animal care takers, who had blue overalls. The experimenter entered into the pen and walked slowly along the walls to make sure all pigs were awake and were paying attention. Then the experimenter stopped at the centre of the wall opposite the entrance with her back against the pen wall, and stood idle in a half circle with a 0.5 m radius which was marked on the floor with blue spray paint. This position was maintained for ten minutes. The experimenter noted the latency in seconds for each pig to approach within the 0.5 m radius with either its head or fore limbs, as well as the latency to touch the experimenter. Pigs that did not enter the radius within the maximum time were given the latency of 600 s (10 min). Tests were recorded by CCTV cameras attached to the ceiling and watched later for the pigs' behaviour.

2.5. Leadership

Within each group, leadership was assigned to individuals who were the first to touch the human in the HAT. When multiple individuals touched the human at exactly the same time, leadership was assigned to each of them. In case none of the pigs touched the human, no leader was assigned. Individuals who attained a leadership position across the three test days were categorized as "consistent leader" whereas the other leaders were categorized as "inconsistent leader". All other pigs were assigned as followers. For each test day a leader was assigned, and a note was made of changes in their role (leader or follower). The three repeated observations per individual were used to calculate repeatability of leadership. To analyse the factors that may predict leadership, the analysis was based on the first test out of three in which a leader was apparent. A group with a "distinct leader" was classified as a group in which one animal was the leader instead of several individuals touching the experimenter simultaneously. Six groups were discarded from this analysis due to having no distinct leader on any of the three tests (multiple consistent/inconsistent leaders on each test day). Thus, data by individual contained information on whether the individual was a consistent leader, inconsistent leader, or follower on each test day. Data by group classified whether groups had a distinct leader (consistent or inconsistent) on each test day.

2.6. Statistical analysis

Data were analysed with R version 4.1.3 (R Core Team, 2023) using two datasets. Dataset 1 had repeated measures per individual over three test days, which was used to assess repeatability (n = 366 individuals across 32 groups). Dataset 2 was analysed by individual with a single binary outcome (leader / follower) at the individual level for the first test in which a distinct leader was present (only for the groups that had a distinct leader in at least one HAT, n = 289 individuals from 26 groups). In dataset 2, six groups were discarded due to lack of a distinct single leader. P-values ≤ 0.05 were considered significant.

Repeatability of leadership (binary value) was analysed using Dataset 1 with "rptR" package (Stoffel et al., 2017) for repeatability analysis with 1000 bootstrapping and datatype as "Binary". The model included body weight at weaning (in kg, at week 4) and sex (male / female), coping response (number of struggles) as fixed factors and pig ID and group ID as random effects. The relationship between leadership, backtest outcome and body weight was analysed using Dataset 2. Leadership (yes / no) was the response variable in a generalised linear mixed model using the "lme4" package (Bates et al., 2015) with logit link for binomial data. Latency to touch the human was the response variable. The predictor variables were body weight at weaning, sex and coping response. For coping response both the number of struggles and vocalizations were entered in the model. Due to the correlation between both (Spearman correlation: $r = 0.75$; $p < 0.001$) only the number of struggles was retained, based on the best model fit (lowest AIC and BIC values). Batch (i.e., cohort) and group within batch, were included as random effects. Post-hoc pairwise comparisons were performed to compare the differences between the levels of the categorical variable (sex) using the "emmeans" package (Lenth, 2021) with response scale in R.

3. Results

3.1. Repeatability of leadership

On the first test day, most groups (22 groups) showed no clear distinction between leaders and followers as 43 % of the pigs did not touch the human. Leadership at the individual level was repeatable but only marginally ($R = 0.095$; $p < 0.001$), which was similar at the group level ($R = 0.202$; $p < 0.001$).

Across three days of tests, 18 pigs from 11 groups attained a consistent leadership position. Six groups had a single consistent leader while five groups had multiple consistent leaders that were equally fast in the test. The remaining groups did not have pigs that attained a consistent leadership position. Post-hoc analysis showed that the latency to touch the human decreased across test days within followers and leaders (Fig. 1). For followers, all pairwise comparisons between days were significant ($p < 0.001$). The followers were also quicker across test days in completing the task right after the leader (day 1: 39.3 ± 6.40, range: 1– 487 s; day 2: 27.9 ± 5.93, range: 1– 548 s; day 3: 16.2 ± 3.30, range 1– 520 s). The latency to touch the human significantly differed, in the post-hoc pairwise comparison within leaders, between day 1 and 2 ($p = 0.032$) and day 1 and 3 ($p = 0.008$), but not between day 2 and 3 ($p = 0.817$).

3.2. Predictors of leadership

The number of struggles, as an indicator of coping style, was not a significant predictor of leadership ($b = -0.361 \pm 0.21$; $z = -1.7$; $p = 0.08$). Similarly, body weight at weaning did not predict leadership ($p > 0.91$). Body weight did not differ significantly between males and females ($p = 0.246$). However, females were more often leaders than males, as shown by a negative association between males and leadership (GLMM: estimate = −1.41; z-value = −2.91, n = 289; $p = 0.003$). From the 26 leaders (classified as leader based on touching the human first on day 1), only six were male. Post-hoc analysis showed that the probability for females to be classified as leader was 0.137 ± 0.029 while for males this was 0.037 ± 0.015, resulting in a 4.13 greater odds for females to attain a leadership position.

4. Discussion

Leaders take a risk by being, for example, the first to explore a new situation. In the Human Approach Test, pigs which were not deliberately socialized to humans took a risk by approaching an unfamiliar human. As seen from the latencies to touch the human, many pigs did not touch the human until the third exposure to the same situation, suggesting they perceive it as a risk. The leaders stood out with a remarkably shorter latency than the followers. Leadership was only marginally repeatable, with 6 out of 26 groups having a consistent single leader across the three test days. Leaders could not be predicted based on their earlier coping response in the backtest or by their body weight (as proxy of dominance). However, females turned out to be much more frequently the leader than the males.

No *a priori* prediction was made regarding sex differences in leadership. Adult and sub adult pigs do show sexual dimorphism in physical appearance (Konjević et al., 2008) and behaviour (Camerlink et al., 2022) but in young pigs, as studied here at six weeks of age, there are only subtle differences between males and females. It was therefore not expected that females would take a leadership role more often. In contrary, based on the larger body weight of males and their dominant position in fights (Camerlink et al., 2022) it was rather expected that males would take the leadership role. The leadership role of females does correspond with the situation in the wild, where a mature wild boar female leads a small herd (Podgorski et al., 2014) while wild boar males are mostly solitary except for during the breeding season (Maselli et al., 2014). In other species, such as Orca and elephants, female lineages are also important in the leadership of groups, especially during food scarcity (McComb et al., 2001; Brent et al., 2015). While in the current study the females were still very young, it has been observed that young female wild boar may form social groups in the absence of an adult female (Bieber et al., 2019), suggesting that there is leadership in group-living females. Females did not differ in body weight from males, which may explain why body weight did not predict leadership.

While the repeatability of leadership was significant but of negligible strength, 6 out of 26 groups (23 %) had a consistent leader across the three days. The low repeatability may be because the data over which it

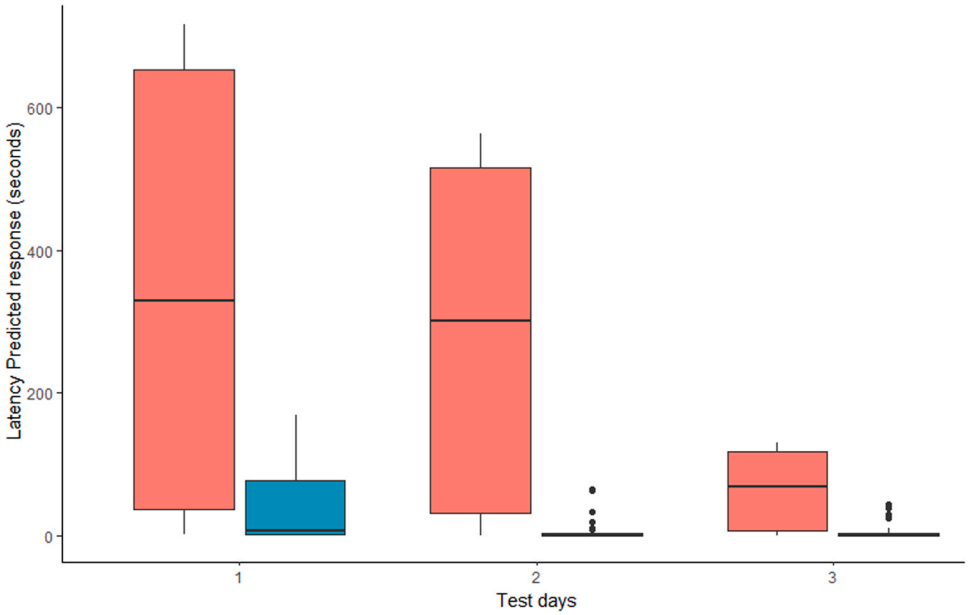

Fig. 1. Boxplot of the predicted latency (fitted value of the response variable), in seconds, of leaders (blue) and followers (orange) to touch the human in the Human Approach Test, across the three test days.

is calculated contains predominantly followers. However, variation in leadership is found to be common across species, suggesting that individual's leadership position can be contextual. Georgopoulou et al. (2022) showed that across two trials stickleback fish show an emerging trend of repeatable leader-follower dynamics in a coordinated movement during an ordered state as compared to fish in uncoordinated (i.e. disordered) movement. Further, certain female mallard were consistent leaders within and between trials when moving in groups (Bousquet et al., 2017). The small but significant repeatability can be indicative that pigs might use distributed leadership within the group, in contrast to personal leadership (Leca et al., 2003). Alternatively, they may switch leadership position randomly as has been observed in sheep (Gómez-Nava et al., 2022), or switch between the leader and follower position based on the environment as was shown in captive house sparrows (Tuliozi et al., 2021). Understanding the dynamics of leader and followers beyond the individual level may contribute to a better understanding of the behavioural complexities found in animal groups.

In this study, we did not find an association between coping style and leadership. A reason for this might be that the response in the backtest relates to different traits than those seen in the HAT despite both involving a response to a potential predator, as discussed by Spake et al. (2012). The backtest, although frequently used as a personality test for young piglets (Finkemeier et al., 2018) due to its heritability and repeatability over time (Zebunke et al., 2017), has been criticized due to the lack of correlation with other personality tests (O'Malley et al., 2019). Nevertheless, the backtest response has shown association with immune responses (Oster et al., 2015) and the response of the autonomic nervous system during general behaviour and in response to human contact (Krause et al., 2017). Krause et al. (2017) showed that reactive pigs in the backtest (no or few struggles, i.e. 'low resisters') had a longer latency to approach and touch a (familiar) human than proactive pigs, but only in the first three days of the experiment and not later on. This suggests that the effect of coping style may be context dependent. Knowledge of factors associated with leadership can increase the understanding of decision making processes across different contexts.

Ramos et al. (2021) have suggested that, with the incorporation of leadership information, domestic and wild groups can be managed better. For example, in goats, old and experienced individuals lead the social herd during grazing, which has resulted in the recommendation to provide leading goats with bells to facilitate group cohesion (Miranda-de la Lama and Mattiello, 2010). Various cities in Europe and beyond face challenges to public health and well-being due to human-wild boar conflicts, and conflicts with other species (Licoppe et al., 2013; Massei et al., 2015; Linnell et al., 2020; Valente et al., 2020; Pokorny et al., 2022), for which management strategies are needed to reduce conflicts. Hence, understanding the factors associated with leadership can help to understand pigs' social structure and manage them accordingly.

In conclusion, we did not find an association between early life individual characteristics and animals' likelihood to attain a leadership position in a novel situation. However, the sexual dimorphism in leadership behaviour offers insight into the social system of domestic pigs.

Funding

The data were part of a research project funded by the Biotechnology and Biological Sciences Research Council (BBSRC, grant number BB/L000393/1). SRUC received funds from the Scottish Government Strategic Research Programme. SK and IC received funding from the National Science Centre Poland (NCN) (grant number 2020/39/B/NZ8/02508).

CRediT authorship contribution statement

Sunil Khatiwada: Writing – original draft, Formal analysis, Data curation. **Simon P Turner:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Marianne Farish:** Writing – review & editing, Methodology, Investigation, Data curation. **Irene Camerlink:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization.

Declaration of Competing Interest

None.

Data availability

Data will be made available on request.

Acknowledgements

We thank the technical staff and students who helped in collection of the data.

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Journal Pre-proofs

Is social support mediated by social relationship strength in pigs?

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PII: S1751-7311(25)00276-9
DOI: https://doi.org/10.1016/j.animal.2025.101693
Reference: ANIMAL 101693

To appear in: *Animal*

Received Date: 13 July 2025
Revised Date: 15 October 2025
Accepted Date: 16 October 2025

Please cite this article as: S. Khatiwada, P. Seddaiu, A. Jaszczyk, I. Camerlink, Is social support mediated by social relationship strength in pigs?, *Animal* (2025), doi: https://doi.org/10.1016/j.animal.2025.101693

Is social support mediated by social relationship strength in pigs?

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Highlights

- We investigated if the strength of a social relationship matters for social support
- Pigs (n=32) were with a familiar pig of strong or weak relationship during a stressor
- The strength of the relationship influenced behaviour and vocalisations
- Saliva cortisol concentrations were unaffected by the relationship strength
- Keeping penmates together during stressful events is recommended for welfare

Abstract

Social support from an individual to another can act as a buffer against stress (i.e. social buffering) for the recipient. While it is known that many species are sensitive to social buffering, including farm animals, the role of the social relationship strength remains largely unclear. The aim of this study was to investigate whether the behavioural and physiological responses of an animal exposed to a stressor were influenced by the strength of the social relationship to the partner present during the event. We hypothesized that pigs with a strong social relationship to the partner (buddy) would show a reduced stress response. Focal pigs (n=34) of four months old were exposed to a mildly stressful scenario (being alone in a weighcrate), followed by the presence of a sibling with either a strong or weak prior social association. Behavioural indicators of stress and social behaviour were recorded, alongside salivary cortisol concentrations at four time points. Pigs paired with a sibling with strong relationship had less often their snouts in proximity, and for a shorter total duration, and had less often their heads in proximity. They also made more low pitch vocalizations. Cortisol concentrations increased following the event, but no significant differences were observed between treatment groups. Buddies mostly remained calm but showed variation in their contact seeking behaviour. Female buddies differed from males in their ability to provide social support. These findings suggest that the relationship strength has an influence on the stress-related behaviour of the focal pig but may not be sufficient to elicit measurable hormonal changes. Overall, the results indicate that social relationships between pigs are complex, with close companionship being important for their ability to cope with stressful events.

Keywords. Social buffering, social facilitation, social bonds, Sus scrofa, relationship strength

Implications

Through social buffering, animals may derive benefits from the presence of a familiar partner during a stressful event. However, in farm practices, animals are often separated from their social group, which may exacerbate stress responses. We found that the strength of the social relationship between familiar pigs influences their stress-related behaviour, but not stress physiology in terms of cortisol concentrations. This suggests that maintaining stable social relationships can improve animal welfare. In practical terms, keeping familiar pigs together, especially during stressful procedures such as regrouping and transport, can reduce stress in farm environments.

Introduction

The strength of social relationships between individuals has been shown to provide various benefits, including increased birth rates and infant survival (McFarland et al., 2017) as well as enhanced thermal regulation (McFarland et al., 2015). Strong social relationships can also be advantageous in adverse situations, by offering security and support to conspecifics. One direct benefit of such relationships is the provision of social support, which is referred to as social buffering when it protects the individual from impaired well-being due to stress (Cohen and Wills, 1985). Social buffering occurs when the *"presence or actions of a bond partner reduces or eliminates the stress response in another individual"* (Crockford et al., 2017). According to social buffering theory (Cohen and Wills, 1985; DeVries et al., 2003), the presence of a social partner, such as a mother, pair mate, or other conspecific, can mitigate stressors such as social separation (Hodges et al., 2014; Hostinar et al., 2014; Rukstalis and French, 2005), predation (Vogt et al., 1981), and exposure to novel environments (Hennessy et al., 2006), ultimately reducing psychological stress (Procidano, 2013). Social support has been documented in a range of species (Massen et al., 2010) and several farm animal species (Rault, 2012). This has demonstrated that companions can indeed reduce stress responses in social partners (Meehan et al., 2017; Wittig et al., 2016; Færevik et al., 2006).

The extent to which social support is effective may depend on the nature of the relationship between individuals. Preston and de Waal (2002) argue that support is more likely to be provided to closely bonded conspecifics. Social bonds can enhance longevity, offspring survival (baboons: Silk et al., 2009; 2010), and reproductive success (feral horses: Cameron et al., 2009), and can exist between mother and offspring (Newberry and Swanson, 2008), breeding pairs (Bales et al., 2021), and peers (Verspeek et al., 2019; Lee and Beery, 2021). The presence and quality of these relationships may vary (Whitehead, 1997), with strong social relationships involving high emotional exchange and affiliative behaviour, while weaker ties represent more distant connections, such as acquaintances or indirect links (Sandstrom and Dunn, 2014; Brent, 2015). The quality of the social relationship is therefore expected to influence the degree of social support that is provided, as was shown in guinea pigs (Kaiser et al., 2003). However, for most species it is currently unknown whether the strength of a social relationship affects social support, and social buffering during stressful events specifically.

Pigs (*Sus scrofa domesticus*) kept in farm conditions are frequently exposed to stressful events, such as new environments, social separation and regrouping. Pigs

can form preferential affiliative relationships (Durrell et al., 2004; Goumon et al., 2020; Clouard et al., 2024) and are responsive to social support (Kanitz et al., 2014; Reimert et al., 2014; Kroell et al., 2025). These studies have shown that pigs respond to the distress of others (Moscovice et al., 2023) and gain support from having a conspecific nearby during a stressful event (Reimert et al., 2014), in particular from a familiar conspecific (a littermate) as compared to an unfamiliar pig (Kanitz et al., 2014; Tuchscherer et al., 2016; Söderquist et al., 2023). This suggests that keeping familiar pigs together during stressful events may be beneficial to them, as has been shown by keeping littermates together at weaning (Camerlink et al., 2021). While the studies of Kanitz et al. (2014) and Söderquist et al. (2023) show that social buffering in pigs does depend on whether there is a prior social relationship or not, they do not reveal whether the strength of an existing social relationship matters. Previously this was explored in young pigs at weaning (Camerlink et al., 2023), but no statistically significant stress buffering effect was found based on relationship strength, possibly due to insufficient contrast between weak and strongly associated littermates. It therefore remains to be explored whether relationship strength matters in social buffering. The aim of this study was to investigate whether the strength of a social relationship influences the magnitude of social buffering during a stressful event. We studied this in pigs which were exposed to a stressful event of being confined in a weigh crate, while there was a sibling nearby with either a strong or weak social relationship. We hypothesised that dyads with strong social relationships show a reduced stress response as compared to dyads with weaker relationships.

Material and methods

Animals and housing

In total 68 pigs participated in the study, of which 34 were focal animals. The sample size was determined based on the values reported by Reimert et al. (2014), using an online sample size calculator with an alpha of 0.05 and a power of 90%. Three pigs were removed from the analyses due to an inconsistency in the test set-up or missing samples, therefore, n = 31 focal pigs for analyses. Pigs were from the Puławska breed and were studied at on average 16 weeks of age (4 months; range 15-18 weeks). Focal animals were females (gilts) while the support buddy (i.e. companion pig) was a male (uncastrated male; n = 24) or female (n = 10) depending on the available pigs within the research criteria. We chose females as focal pigs to reduce variation due to sex, while from an ecological perspective females are expected to be more attuned to social presence than males, which in nature would be largely solitary from adulthood (Podgórski et al., 2014). Pigs were born in free farrowing pens and kept together as a litter without cross-fostering. They were weaned between 4 and 5 weeks of age. From 6 weeks of age, pigs were assigned to enriched (n = 14) or barren (n = 18) housing conditions, which was part of an overarching research question and was balanced across social support treatment. All pigs were housed in a 6 m^2 pen (2 × 3m) with a solid floor. Barren housed pigs had two static enrichment items (metal chain and sisal rope hanging from the wall) and no substrate. Enriched housed pigs had straw bedding and received each week a novel object and a fresh manipulable object, from 2 weeks of age until the end of the study. Pens were cleaned every other day and the enriched pens received fresh straw after cleaning. Pigs received ad libitum commercial pig feed suitable to their weight category and had *ad libitum* access to water.

From 6 weeks of age, litters with more than five pigs were randomly split into two separate groups and remained in this group composition until the test. This created for the social support test variation in relationship strength, whereby some sibling pairs for the test were continuously housed together whereas other sibling pairs were composed of one pig of each group, thus being housed together only for the first 6 weeks of life. This difference in relationship strength between siblings formed the contrast (treatment) for the social support test. The social relationship treatment was balanced for housing conditions, with for the strong social treatment a 1:1 enriched:barren ratio and for the weak social treatment a 1:1.8 ratio.

Social support test

The 34 focal pigs were tested across five batches (cohorts) between June 2023 and June 2024. The test was based on Reimert et al. (2014). However, based on a pilot study the test duration was reduced from 15 to 4 minutes as a refinement to the procedures, to remain below the endpoints set for the ethical treatment of animals. Due to regular cognitive tests as part of the overarching project, all animals were accustomed to human handling and trained to go into the test room alone for at least 5 minutes, which was previously associated with a food reward. Therefore, all pigs were well habituated to the test room whereas being in the weighcrate was expected to result in a stressor.

The test room was 3.5 × 3.5 m with solid walls and one entry gate. A metal weighcrate (dimensions in length × width × height: 1.22 × 0.60 × 0.60 m in batch 1 and 1.45 × 0.53 × 0.85 m in other batches) was placed in the centre of the room, facing a wall (Figure 1). The tiled floor was bedded with a small layer of straw (without straw in the crate). The focal pig was led from the home pen to the test room (circa 30 m distance) and led into the weigh crate. The test was started and the focal pig remained for 1 minute on her own in the test room (with the aim to arouse a mild stress), here referred to as the solitary phase (Figure 1). After 1 minute, a buddy pig was brought into the test room for social support, starting the social phase. The buddy was either a sibling from the same social group (penmate) as the focal pig (strong relationship) or a sibling from another group (weak relationship), which formed the main treatment. Where possible, the selected buddy was a male with lower body weight than the focal pig to avoid dominance threats to the focal animal. Due to an uneven sex distribution in the population, 24 buddies were male (15 strong; 9 weak treatment) and 10 were female (5 strong; 5 weak). Buddies were only used once in the test and never tested as focal pig. The buddy was free to walk around in the test room and could interact with the focal pig through the bars of the weigh crate. At 3 minutes after the entry of the buddy (4 mins in total) the test was ended and both pigs were returned to their home pen. The test room was cleaned in between tests. Tests took place between 10 am and 4 pm. Dyads of each treatment were balanced across the day to avoid a confound between daytime and treatment. None of the pigs reached the endpoints that were set to terminate the test early in case of excessive stress responses (escape attempts or hyperventilation).

Social differentiation test

To verify whether the focal pigs still recognized their former pen mates (either based on familiarity or kin recognition; Stookey and Gonyou, 1998), and whether they distinguished them from completely unfamiliar pigs, they were observed in a regrouping situation. The day after the social support test, all focal pigs (within a batch) were grouped together with at least one sibling from their home pen, one

sibling from a different pen, and an unfamiliar pig of the same age (no sibling or pen mate). This resulted in a group of 13-14 pigs per regrouping situation. Pigs were marked with an animal marker crayon (Raidex, Germany) for individual recognition. The regrouping arena was 12 m^2 (3 × 4 m) with a solid floor and fresh straw bedding. An overhead camera recorded the behaviour. The test lasted for 45 minutes after which all pigs were returned to their home pen. The frequency and duration of fights of the focal pigs were observed from video by a single observer, while noting the identity of the opponents, which enabled calculation of whether they fought with unfamiliar pigs, penmates or siblings from a different pen more often than expected by chance.

Saliva sampling and cortisol analysis

To assess the stress response of the focal pig, saliva samples were taken at four time points (**t**): just prior to the test (t0), directly after the test (sample taken when the pig was still in the crate) (t4), and at 30 (t30) and 60 minutes (t60) after the test, when they were back in their home pen (Figure 1). Samples were collected using the Salivette® Cortisol synthetic swab with Salivette® Cortisol tube (Sarstedt, Germany, catalogue number 51.1534.500). The swab was secured with a plastic zip tie that was held at all times by the researcher to prevent the pig from swallowing the swab. During the preparation, collection and storage of the samples the handlers wore disposable latex gloves to avoid contamination of the sample. The swab was introduced in the pigs' lower cheek, letting it free to open or close the mouth. The swabs were left in the mouth for 40 seconds. If the animal rejected the swab by spitting it out then the swab was reintroduced. The swab was then placed in the Salivette® tube and placed in a styrofoam box with ice. Within 3h after collection, samples were transferred to a -80ºC freezer and stored until laboratory processing. For analysis, the collected saliva samples were thawed on ice and centrifuged for 10 minutes at 2000 × g at +4°C. Next, the saliva was transferred to sterile 2 ml Eppendorf tubes and subjected to a second centrifugation for 20 min at 1500 × g at 4°C. The supernatant was collected and used for further analysis. Cortisol concentrations were measured using an ELISA assay (Saliva Cortisol (Expanded Range) Enzyme Immunoassay Kit, Salimetrics, USA, catalogue number SAL-1-3002), following the manufacturer's instructions. Each sample was analyzed in duplicate. Each plate included six standards with known cortisol concentrations and a blank sample containing no cortisol. To minimize inter-assay variability, all samples from the same individual were analyzed on the same microplate. Absorbance was measured at 450 nm using a microplate reader. For each sample, two independent optical density readings were obtained and averaged. The binding ratio was calculated, where the mean optical density of the sample is divided by the mean optical density of the blank sample. Cortisol concentrations (µg/dL) were interpolated from a standard curve fitted using a four-parameter logistic regression model suitable for ELISA data. All calculations were performed using R software (R Core Team, 2023) (version 4.2.3).

Behavioural observations and vocalizations during the social support test

An overhead CCTV camera recorded the test from above while a sports camera (GoPro) recorded the sound and the view facing the pig's head. The overhead video was used for recording behaviour and the front-facing camera was used for scoring vocalizations. The behaviour of the focal animal was recorded using the ethogram described in Table 1. The initial ethogram also included lying, sitting, escape

attempts and urinating (following the ethogram described in Reimert et al., 2014), but were removed as these behaviours did not occur. Behaviours were scored as frequencies, and additionally the duration of head proximity and snout proximity was scored in seconds (Table 1). For the non-social behaviours (standing alert and attempting to turn) a distinction was made between the solitary phase (first 1 min.) and the social phase (3 min. directly after). The observation started as soon as the door of the weigh crate was closed and ended when the buddy was removed (having its front legs outside the room). Behaviours were scored using Windows media player.

Audio recordings of vocalizations were available for 18 pigs (10 males and 8 females, balanced by treatment) due to a technical error with the camera on some test days. High- and low pitch vocalizations of the focal pigs were coded manually in Boris V.8.21.8 (Friard and Gamba, 2016). High-pitched vocalizations included screams, squeals and grunt-squeals while low-pitched vocalizations included short and long grunts (Reimert et al., 2014). Each single vocalization was scored as an event, without recording the duration, and summed by pig to obtain the total amount of vocalizations.

To account for the behaviour of the buddy, the duration (in seconds) of the buddy being in direct proximity (<30 cm) of the weighcrate was recorded (Video S1). The observation started as soon as the buddy had its two front legs in the room and ended as soon as its front legs were outside the room. Additionally, the behaviour of the buddy was scored using a 3-point scale: 1) Calm: engaged in exploration, walking, or social contact. Does not show stress-related behaviour (see 2 and 3); 2) Restless: spends time at the exit and may push the exit door with its snout. May show defecation or freezing behaviour; 3) Stressed: showing signs of distress, including escape attempts by climbing the exit door with the front legs or jumping against the door.

The videos were observed by a single observer, who performed intra-observer reliability on 20% of the videos. Inter-observer reliability was conducted by another observer scoring 20% of the videos, and the values were compared with Pearson correlations. The intra-observer reliability was 0.92, and inter-observer reliability 0.99, therefore showing excellent agreement.

Statistical analyses

Data were analysed using linear mixed models and generalised linear mixed models in R version (4.3.2) (R Core Team, 2023). The “lme4” package (Bates et al., 2015) was used (unless stated otherwise) to perform linear mixed models with a Gaussian distribution. The “lmerTest” package (version 3.1-3) (Kuznetsova et al., 2017) was used to perform a generalised linear mixed models with Poisson distribution, and negative binomial distribution. Stepwise backward regression was performed on the full models to select the best fitting model based on the lowest Akaike Information Criterion. Models were assessed for diagnostics including uniformity in residuals, overdispersion, and zero-inflation. The residuals of the model were assessed from Shapiro-Wilk statistics. Homoscedasticity was assessed via visual inspection of residual plots against fitted values. Cook distances were calculated and plotted to identify influential data points (threshold set at 1). Multicollinearity detection was performed using the variance inflation factor, using the “car” package (Fox and Weisberg, 2019). The variance inflation factor did not indicate strong multicollinearity (<2) in any of the models. Post-hoc comparisons were conducted using the “emmeans” package (Russell, 2020) to obtain the least square means (**LSmeans**)

with SE. Values were considered significant at <0.05. All data figures were made in R using the “ggsave” function from the “ggplot2” package (version 3.5.1) (Wickham, 2016).

Analysis of behaviour

The behaviours aggression, defecation, and tail posture showed too little variation to enable analysis and were therefore presented descriptively. However, a binomial test was performed to confirm if these behaviours were chance occurrences or not. The frequency of standing alert and turning behaviour from the social phase (3 min.) was scaled to one minute to match the duration of the solitary phase, and was thereafter compared using the Wilcoxon signed-rank test. The Shapiro-Wilk test was used to determine the normality of the distribution of standing alert and turning behaviour.
The duration of snout proximity was analysed as a response variable in a linear mixed model, using the “nlme” package (Pinheiro et al., 2023) (version 3.1-164). The predictor variables were social treatment (strong / weak relationship), housing condition (barren / enriched), and sex of the buddy (male / female), with the frequency of turning and standing alert in the social phase as covariates. Group, nested within batch, was included as a random effect. Snout proximity shown by the focal pig correlated moderately with spatial proximity of the buddy ($r = 0.489$, $p = 0.005$), and therefore, proximity from the buddy was excluded from the model to avoid multicollinearity. The best-fitting model included only the social treatment.
The duration of spatial proximity of the buddy was analysed as a response variable in a separate linear mixed model to examine whether the buddy was influenced by the focal pig. The predictor variables were the social treatment, sex of the buddy, and the sum of stress-related behaviours of the focal pig (sum of tail down, aggression, turning, standing alert, and defecation). Group, nested within batch, was included as a random effect.
The frequencies of head proximity, snout proximity, turning and standing alert were analysed as response variables in generalised mixed models with Poisson distribution, as the response variable was count data (without zero-inflated frequency). The predictor variables were social treatment, housing condition, and sex of the buddy. Turning and standing alert were added as covariates in the models of head and snout proximity. Group nested within batch was included as a random effect. The best fitting model for head proximity included the social treatment, sex of the buddy, and standing alert. The best fitting model for snout proximity included the social treatment, housing condition, and turning behaviour. For turning and standing alert the full models were retained.

Analysis of vocalizations

The frequency of vocalizations was divided into the solitary phase (1 min.) and the social phase (3 min.), whereby the vocalizations from the solitary phase were used to ascertain whether differences between the treatment groups were not already existent before the treatment started. Low pitch vocalizations in the solitary phase and social phase were analysed as response variables in generalised mixed models with Poisson distribution. For the analysis of vocalizations only, we performed a forward step selection from the null model to select the best fitting model, and model diagnostics were performed using the “DHARMa” package (version 0.4.6; Hartig, 2022). High pitch vocalizations were analysed as response variables in a generalised mixed model with negative binomial distribution to account for heteroscedasticity. The predictor variables for both the low pitch and high pitch

variables were the social treatment, housing conditions, sex of the buddy, the focal pigs' body weight (with quadratic term included only for low pitch model), as well as the interaction between treatment and body weight (as body weight influences vocalizations in pigs: Garcia et al., 2016). Group ID was included as a random effect. The quadratic term for body weight during low pitch vocalizations was included as body weight did not show a linear association with low pitch vocalizations, which was also confirmed by examining the residuals. The full models were retained as best model fit.

Analysis of cortisol concentrations

The cortisol values for t0, t4, t30, and t60 were subtracted from each other to obtain the difference between each two consecutive time points. The values were then divided by the initial cortisol value at the time point to obtain a proportional change in cortisol values. This resulted in three values per pig, which were analysed as repeated values in a linear mixed model to test if the changes in cortisol concentration were influenced by any of the predictors. Both the original cortisol values (t0, t4, t30, and t60) and the proportional change (t0-t4, t4-t30, t30-t60) were analysed in a linear mixed model with social treatment, housing condition, sampling period and daytime (am / pm) as predictor variables and body weight of the focal pig as covariate. Pig id (to account for repeated measures) and group id were included as random factors.

Analysis of social differentiation

Dyadic fights were classified into three groups: fights between unfamiliar pigs, between siblings who were kept together as pen mates, and between siblings that were separated (not penmates). Since the group composition at regrouping varied slightly between batches, we calculated for each individual the probability of encountering pigs from each familiarity category and averaged the expected proportion per batch. A one-sample proportion test, using the prop.test() in R for an expected proportion (here based on mean encounter), was tested under the null hypothesis using a chi-squared statistic to test the differences in the number of fights for the categories.

Fight duration was analysed as a response variable in a generalised mixed model with a Gamma distribution (as the duration was not uniformly distributed). The predictor variables were the familiarity category (unfamiliar, siblings kept together and siblings separated), same sex dyad (yes / no), sex of the initiator (male / female) and the difference in body weight between opponents, with group as a random effect.

Results

Behaviour of the focal individual

All but one pig showed at least one of the stress-related behaviours of trying to turn around in the crate or standing alert (freezing). Attempts to turn around in the crate occurred more frequently before the entry of the buddy (mean ± SD: 2.3 ± 2.22) than when the buddy was present (0.7 ± 0.55) (Wilcoxon signed-rank test: $z = -3.34$, $n = 26$; $p < 0.001$). Standing alert did not differ significantly between the solitary and social phases ($z = -1.78$, $n = 27$; $P = 0.08$). Aggression, tail down, and defecating occurred infrequently (Table 2), but were significantly different from chance (aggression: $z = -4.66$, $n = 31$, $P < 0.001$; tail down: $z = -1.79$, $n = 31$, $p = 0.02$; defecating: $z = -2.51$, $n = 31$, $P = 0.003$).

Pigs paired with a buddy with a strong social relationship had a shorter duration of snout proximity and less frequent snout proximity and head proximity (Table 2). The social treatment did not influence the frequency of turning or standing alert (Table 2). Regardless of the social treatment, pigs that were attempting to turn more frequently in the crate showed less snout proximity (b = -0.26 ± 0.092 times; P = 0.004). Similarly, pigs that were more often standing alert had less head proximity to the buddy (b = -0.139 ± 0.062; P = 0.03). Focal pigs that had a female buddy had more frequent head proximity than those with a male buddy (female buddy: 7.13 times, male buddy: 5.04 times, SE = 0.241, P = 0.04) while the difference in snout proximity was not statistically significant (female buddy: 3.22 ± 0.664; male buddy: 2.04 ± 0.373, P = 0.09). Further, pigs from barren housing conditions were more likely to have snout proximity with the buddy than pigs from enriched pens (barren: 3.33 times, enriched: 1.97 times, SE = 0.418, P = 0.03).

Vocalizations

Pigs (n = 18) made frequent high and low pitch vocalizations, both in the 1 min. solitary phase (mean ± SD high pitch: 2.3 ± 4.80, low pitch: 18.4 ± 9.59), and in the 3 min. social phase (high pitch: 9.9 ± 14.19, low pitch: 37.0 ± 19.32; Fig. 2a). In the solitary phase, when the treatment was not yet in effect, pigs from the different treatments did not differ in their frequency of vocalizations (Fig. 2a; P >0.05). During the social phase, the frequency of low pitch vocalizations depended on an interaction between social treatment and body weight, whereby heavier pigs from the strong social treatment made less low pitch vocalizations (Fig. 2a; P < 0.001). Overall, pigs in the strong social treatment made 2.21 times more low pitch vocalizations than pigs from the weak treatment (strong: 56.5, weak: 25.6, SE = 0.356; P = 0.002) but did not differ in the frequency of high pitch vocalizations (strong: 4.03, weak: 10.04, SE = 0.326; P = 0.26) (Fig. 2b).

Focal pigs which were paired with a male buddy made 9 times more high pitch vocalizations than when paired with a female (female buddy: 2.07, male buddy: 19.58, SE = 0.099; P = 0.01) and 1.5 times more low pitch vocalizations (female buddy: 31.5, male buddy: 45.9, SE = 3.46, SE = 6.08; P = 0.02; Fig. 2c). Pigs housed in barren housing conditions emitted more low pitch vocalizations compared to pigs from enriched conditions (barren: 45.3, enriched: 31.9, SE = 0.224, P = 0.03).

Cortisol

The saliva cortisol concentrations increased at t30 and reduced by t60 (P = 0.04) but were generally low across the time points (Fig. 3a). The social treatment did not significantly influence the proportional change in cortisol concentrations (P = 0.96; Fig. 3b). The proportional change in cortisol was also not influenced by any of the other predictor values (housing conditions, body weight: P >0.10).

The behaviour of the buddy

The buddies were in nearly all tests scored as calm (83.9%), or otherwise restless (16.1%, n = 5), but were never scored as stressed (0% score 3). Buddies varied in the duration that they spent near the crate (mean: 119.1 s; range: 59-168s), which was between 32-93% of the test duration. The proximity of the buddy to the crate was not influenced by the social treatment, its sex, housing condition or the behaviour of the focal pig (P > 0.05).

Social differentiation

During the regrouping event to test social differentiation, 165 fights were observed in total (Table 3). The number of fights between unfamiliar pigs (144/165) was above the chance level (Table 3; proportion test: $\chi 2 = 21.22$, df = 1, 95% CI [0.81, 0.91], $P < 0.001$), while fights between siblings kept together occurred below chance level (proportion test: $\chi^2 = 24.34$, df = 1, 95% CI [0.02, 0.09], $P < 0.001$). However, fights between siblings that had been separated did not differ from the expected chance level (proportion test: $\chi^2 = 0.19$, df = 1, 95% CI [0.04, 0.13], $P = 0.65$). The familiarity categories differed in fight duration, whereby dyads of siblings that had been separated fought for shorter duration than unfamiliar dyads (Table 3). There was no difference in the fight duration between unfamiliar dyads and dyads of siblings from the same pen ($P = 0.71$) or between dyads of siblings that were penmates or not ($P = 0.82$).

Discussion

We hypothesised that dyads with a strong social relationship (siblings always housed together) would exhibit less stress than dyads with a weaker relationship (siblings which were separated for at least two months) in a setup where test individuals are kept within a close confinement to induce a mild stress response. During, the solitary phase in the social support test, pigs showed some signs of behavioural distress, which reduced when the buddy entered the test room in the social phase. The social treatment resulted in behavioural differences but did not result in a reduction in the physiological stress response as measured by salivary cortisol.

Indicators of behavioural distress

We expected that pigs in the strong social treatment would show less stress-related behaviour, such as attempts to turn in the weighcrate, standing alert or freezing, defecating and tail down. As in the current study there was no difference between the treatment groups in standing alert and turning behaviour, these behaviours seem uninfluenced by the familiarity of the buddy. Other studies reported up to 42% of pigs showing escape attempts, even with a buddy present (Söderquist et al., 2023), and for up to 20% of the time (Reimert et al., 2014). The lack of such more extreme stress-related behaviours is likely due to the familiarity of the pigs with the test room and their habituation to previous test circumstances Aggression, tail down, and defecating occurred too infrequently to analyse, which further supports the observation that pigs did not show extreme behavioural responses. Other common indicators of emotional states in pigs, such as ear- and tail postures (Reimert et al., 2013; Camerlink and Ursinus, 2020; Murphy et al., 2021) were less suitable in this specific study. The Puławska breed has large lob ears which therefore cannot be reliably scored for ear postures, such as ears back during negative emotions (Reimert et al., 2013). The long tail was nearly always in an upward position, therefore likely reflecting arousal rather than fear (Camerlink and Ursinus, 2020).

Less social proximity

The main behavioural differences were found in the duration and frequency of social proximity. Pigs with a strong relationship made less snout and head proximity and had a shorter duration of snout proximity. While we expected pigs with a strong relationship to make more social contact (see for example video S1), the reduced

duration of social proximity may be explained by the familiarity between the pigs. In the weak treatment, the focal pig and buddy were siblings but had not encountered each other for at least two months. Therefore, this is likely to have caused an increased social interest (Meese and Ewbank, 1971). Other studies found that unfamiliar pairs had more social proximity (Söderquist et al., 2023) or social contact (Kanitz et al., 2014) compared to familiar pairs, which may be due to an ambiguous motivation for contact (e.g. aggression; Söderquist et al., 2023). Snout proximity is used for social recognition (Newberry and Wood-Gush, 1986; Camerlink and Turner, 2013) and is known to increase when unfamiliar pigs meet (Camerlink et al., 2022). While the buddy in the weak treatment was not completely unfamiliar, the separation will likely have resulted in the motivation to confirm or re-establish dominance relationships, especially as months had passed (Stookey and Gonyou, 1998; Hoy and Bauer, 2005). As snout and head proximity were scored as behaviours initiated by the focal pig, it may also show that the focal pigs from the weak treatment were seeking more social support than pigs in the strong treatment. While the proximity of the buddy will have influenced the opportunity for contact, focal pigs still had the space to avoid head or snout proximity when the buddy was nearby. Pigs that showed more stress-related behaviour (turning and standing alert) made less snout or head proximity to the buddy, while the buddy did not significantly change its social proximity based on the stress-related behaviours of the focal pig. This may partly be because one behaviour takes away time potentially spent on the other behaviour. However, it may also be that more stressed pigs had less interest in social contact and instead were more driven to try to get out of the crate, although no escape attempts like jumps were made.

Vocalizations

Pigs vocalized frequently, which additionally confirms that the test was perceived as stressful**.** The effect of social relationship on low pitch vocalizations was influenced by an interaction with body weight. Heavier pigs in the strong treatment showed less low pitch vocalizations whereas heavier pigs in the weak treatment made more vocalizations. However, this relationship was driven by few data points of heavier pigs. Heavier pigs may have a higher dominance rank (Drickamer et al., 1999), although not always (Tong et al., 2019), and this may influence how they communicate with animals of different or unknown dominance rank (Seyfarth and Cheney, 2003; Nogueira et al., 2016). As vocal communication is an honest signal of fighting ability in pigs, due to the correlation between body weight and grunt formant frequencies (Garcia et al., 2016), the scenario of the weak social treatment may have encouraged more display of fighting ability by the larger animals. As different low pitch calls vary in their length and frequency depending on the context of the situation (Marchant et al., 2001; Briefer et al., 2022), it would require a more precise analysis of the vocalizations to draw conclusions on this finding. As the sound recordings were not of high quality this was unfortunately not possible for the current data.

Overall, pigs in the strong social treatment made more low, but not high, pitch vocalizations than pigs in the weak treatment during the phase when the buddy was present. Low and high pitch vocalizations occur across contexts of difference valence (Briefer et al., 2022). However, high pitch vocalizations, including screams, squeals and grunt-squeals, are generally observed during stressful events (Reimert et al., 2013). In contrast, low pitch vocalizations, such as short and long grunts, have

a variety of communicative functions. For example, the frequency of low pitch vocalizations may increase during aversive events (Reimert et al., 2013), but grunts are also typical during positive events (Maigrot et al., 2018). The results therefore suggest that the strength of the relationship did not alter stress vocalizations but did affect the general level of communication, with pigs with a strong relationship being more communicative. Along with the less frequent snout proximity in the strong social treatment, this relates to a recent study which found that vocalizations (grunt, squeal or scream together) loaded on the same Principal Component Factor as nose-to-nose contacts but with an inverse relationship (Ambruosi et al., 2024).

Focal pigs made substantially more vocalizations when the buddy was a male rather than a female. As the males were entire males of four months of age, they may have shown increased interest in the female in the crate. The sexual behaviour of boars is characterized by frequent grunts (Hemsworth and Tilbrook, 2007), which may have influenced the females' vocalizations in response. However, we did not find an effect of the buddy's sex on their duration near the crate. Furthermore, all focal females were before their first reproductive cycle and may therefore have had mixed motivations to vocalize.

No difference in cortisol concentration

The concentration of cortisol peaked at 30, minutes after the social support test and reduced thereafter. This shows that there was a physiological stress response related to the test, which is in correspondence with the peak found in other studies using pig saliva (Reimert et al., 2014; Escribano et al., 2015). However, there was no effect of the treatment, or other variables, on the cortisol concentration or the proportional change between the time points (between zero and four minutes, between four and 30 minutes and between 30 and 60 minutes). This is similar to the social support test of Reimert et al. (2014) in which behavioural but no salivary cortisol differences were found between their treatments (with or without penmate or different coping style). The absence of significant differences in cortisol concentrations between the treatment may partly be attributed to the intensity of the stressor and the timing of sample collection. Our sampling protocol followed that of Reimert et al. (2014), with the key difference being the duration of stress exposure (15 minutes in Reimert et al. (2014) versus only 4 minutes in ours) due to welfare considerations. This shorter exposure may have been insufficient to elicit a physiological difference between the treatment groups. In comparison, Reimert et al. (2014) found cortisol concentrations around 2.5 ng/ml (baseline and 60 minutes later) to circa 4 ng/ml at 30 minutes after the test. These values are considerably higher than those found in the current study. The change in the test design was based on a pilot study in different pigs and we had not anticipated that our pigs would be in general much calmer in test situations due to the habituation to various test circumstances and frequent positive human handling (Hayes et al., 2021). However, the absence of an effect of salivary cortisol concentrations does not rule out potential differences. There are various limitations in using cortisol as a single indicator (for example, influences of non-stress related glucocorticoid synthesis; Ralph and Tilbrook, 2016) and using multiple biomarkers such as done by Escribano et al. (2015) may provide different results.

The role of the support buddy

Although focal pigs displayed behavioural signs of stress, such as frequent turning within the enclosure, nearly all buddies remained calm without overt stress-related behaviours. The buddy was free to explore the test room, which had some straw, and the buddy could choose whether to interact with the focal pig or not. Some buddies seemed uninfluenced by the distress of the focal pig, and given the relative short duration of proximity to the weigh crate with the focal pig, showed a lack of interest to approach it after initial social recognition. Still, they maintained for a third to nearly all of the time in social proximity, directly besides the weigh crate. In a study on helping behaviour in pigs, in which the focal pig was trapped, pigs which spent more time watching the focal pig were more likely to help it, while this social attentiveness was uninfluenced by their genetic relationship (sibling or not) (Moscovice et al., 2023).

In two cases in the weak treatment, the pigs engaged in agonistic behaviour rather than social support. We had expected that the stress-related behaviours of the focal pig, most notably the high-pitched vocalizations, would result more in distress in the buddy through emotional contagion (Reimert et al., 2017). Pigs are sensitive to positive and negative emotions expressed by other pigs (Reimert et al., 2017) and may respond with increased social proximity and freezing when confronted with a distressed penmate (Goumon and Špinka, 2016). However, while emotional contagion is argued to assist in inducing social support in animals (Ben-Ami Bartal et al., 2016; Peen et al., 2021), a recent study in pigs did not find evidence for a relationship between emotional contagion in the observer (the buddy) and its effectiveness in providing social buffering (Reimert and Bolhuis, 2024). Maybe more extreme distress, such as in the study of Zhang et al. (2023) where they applied electric shocks, or prior experience of the stressor (Goumon and Špinka, 2016) would elicit more profound social support. Research into pigs' capacity for emotional recognition and empathy-like behaviours (Marino and Colvin, 2015) could provide deeper insight into the mechanisms underlying social support.

Evidence of social differentiation

The regrouping scenario was conducted to assess whether focal pigs differentiated the siblings from different pens from completely unfamiliar pigs. Previous studies have shown that social buffering from completely unfamiliar pigs is less effective than from familiar pigs (Kanitz et al., 2014; Söderquist et al., 2023) and therefore it was important to verify whether the buddies in the weak social treatment would not be seen as strangers. Pigs fought most with unfamiliar pigs, but the frequency of fights with siblings from other pens was not different from chance. However, the fight duration between siblings which had been separated (those who were not penmates) was in fact shortest. This shows that the focal pigs did recognize their siblings in some way, possibly through olfactory cues (Kristensen et al., 2001), after being separated from them for at least two months. Pigs can recognize former group mates after separation of up to at least 25 days (Ewbank and Meese, 1971) but mostly recognize other pigs based on familiarity rather than genetic relatedness (Stookey and Gonyou, 1998). The exact duration to which pigs can recognize former group mates is not well studied, although reintroducing weaned sows back into their initial social group does suggest social recognition persists for longer (Hoy and Bauer, 2005), including recognition of dominance rank (Ewbank and Meese, 1971; Meese and Ewbank, 1973). While there was a similar fight duration between unfamiliar pigs and siblings from the same pen, it has been well established that penmates

recognize each other well (McLeman et al., 2008) and will fight less (Otten et al., 1999; Mesarec et al., 2021) and for shorter duration (Li and Johnston, 2009). However, it is also known that penmates may engage in fights when moved to a new location in an opportunistic attempt to gain a better social position in the new environment (D'Eath et al., 2010).

Other factors of influence

Pigs from barren housing conditions were more likely to have snout proximity with the buddy, but the difference was minimal. Pigs housed in barren conditions are known to make more social contact, which is usually explained by the lack of other distraction in a barren pen (Beattie et al., 2000; Giuliotti et al., 2019). That this is found in the test room may confirm that this heightened social interest persists outside the home environment. Further, notable sex effects were found. While the focal pigs were all females, the buddies were males or females due to an uneven sex distribution in the cohort of buddies to select from. As discussed above, focal pigs vocalized more when the buddy was a male instead of a female. Further, female buddies received more head proximity from the focal pigs than males, thus interacting more. While this was scored from the focal pig's perspective, the interaction depends of course on the social proximity of both pigs. Females have been found to provide more social support (Rault, 2012), in line with the 'tend-and-befriend' theory (Taylor et al., 2000). For pigs this is in line with their ecology of small sister groups while the males are mostly solitary (Podgórski et al., 2014).

Conclusion

This study showed that the strength of the social relationship does have an effect on the behaviour of pigs during a stressful event, most notably on social proximity and low pitch vocalizations. This knowledge can be used during management practices which are known to be stressful events, such as weaning, regrouping, isolation into a sickpen or transport. Ensuring the presence of a penmate specifically may be advantageous during such circumstances.

Ethics approval

The study was approved by the Local Ethics Committee for Animal Experiments, Warsaw, Poland, protocol number WAW2/054/2023.

Data and model availability statement

The data are deposited in an official repository under a CC-BY 4.0 license and are publicly available at DOI: https://data.mendeley.com/preview/s4gwb5893m?a=5e3b4ee8-5b38-4cac-8cfd-8418b2f088f5. Information can be made 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 authors did not use any AI and AI-assisted technologies.

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Declaration of interest
None.

Acknowledgements
We would like to thank Victoria Lee for her recommendations on the experimental design.

Financial support statement
This study was funded by the National Science Centre Poland (NCN), project number 2020/39/B/NZ8/02508. P.S. received funding from National Science Centre Poland (NCN) project number 2021/43/O/NZ8/00711.

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Tables

Table 1. Ethogram for behaviour of the focal pig during the social support test. Social behaviours are only scored after the entrance of the buddy (social phase). Behaviours were scored as frequencies, and snout proximity along with head proximity were additionally scored as duration.

Behaviour	Description
Standing alert (freezing)	Resting on all four legs without moving off its position for > 3 s. Does not engage in any other behaviour. May include freezing behaviour.
(Attempt to) turn	Moves its head in the direction of the opposite site of the crate, thereby curving the body to change position and exerting pressure on the side of the crate. Includes attempts or full turns.
Head proximity	Has its head <30 cm from the head of the buddy, with the heads being in any orientation, except snout proximity.
Snout proximity	Snout of the focal animal is touching or close to touching the snout of the buddy
Aggression	Shows agonistic display behaviour or attempts to bite through the crate. Scored for the focal animal and buddy separately.
Defecating	Poos when inside the crate
Tail down	Tail is uncurled and hanging loosely or being held tightly against the body

Table 2. Percentage of pigs (n = 31) that showed each behaviour, and the average occurrence of each behaviour (Least Square means ± SE) shown by focal pigs during the 3-minute social phase of the social support test. In the social phase, focal pigs were paired with a buddy of either a weak or strong relationship. Values of the behaviour are in frequency unless indicated as seconds (s).

Behaviour	%	Weak relationship	Strong relationship	SE	*P*-value treatment
Standing alert	74.2	1.79	1.93	0.253	0.78
(Attempt to) turn	77.4	2.38	1.59	0.445	0.18
Head proximity	100	7.26	4.95	0.104	0.01
Snout proximity	93.5	3.51	1.87	0.122	0.01
Snout proximity (s)	100	28.5	11.7	5.73	0.01
Aggression	6.5	0.1 ± 0.28	0.1 ± 0.24	n/a	n/a
Defecating	25.8	0.4 ± 0.51	0.2 ± 0.38	n/a	n/a
Tail down	32.25	0.5 ± 0.51	0.2 ± 0.42	n/a	n/a

n/a: not applicable

Table 3. Fight occurrence when regrouping pigs (n=41) in groups of 13-14 pigs. Groups consisted of siblings that are penmates, siblings that are not penmates (separated for at least 2 months) and unfamiliar pigs (which had never encountered each other before).

Dyad composition	Siblings that are penmates	Siblings but not penmates	Unfamiliar pigs	*P*-value
Number of fights	8	13	144	n/a[1]
Average expected chance level for an encounter / realised proportion	0.2 / 0.05	0.07 / 0.08	0.71 / 0.87	n/a
Fight duration (s)	16 ± 6.24[ab]	12.1 ± 4.06[b]	37.1 ± 6.24[a]	<0.001

[1]n/a: not applicable

[ab] Values within a row with different superscripts differ significantly at $P<0.05$.

Figure captions

Figure 1. A schematic timeline of the social support test conducted with 4-month-old pigs (t0 - t4 are at double scale).

Figure 2. A boxplot showing the effect of the social relationship treatment on the vocalizations of focal pigs (n =18) during the social support test. Figures show A) the interaction between body weight (kg) and the frequency of low pitch vocalizations based on social relationship treatment, with a 95% confidence interval (CI); B) the frequency of vocalizations in the solitary phase (1 min.) and social phase (3 min.);

and C) the frequency of vocalizations (high and low pitch) in the presence of a female or male buddy in the social support test, by social relationship treatment.

Figure 3. Salivary cortisol concentration of focal pigs (n = 31 females). Figures are A) per time point (t0: before the social support test; t4: 4 minutes after the test; t30 and t60: 30 and 60 minutes after the test in the home pen, respectively) and B) per time period (difference between time points).