Significance of social touch in pigs' behaviour, health and fitness

Wpływ dotyku społecznego na zachowanie, zdrowie i sprawność świń

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List of included publications

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Summary

The need for physical contact has received increasing attention in recent years across several species, particularly following the social restrictions imposed during the COVID-19 pandemic. In social species, physical contact plays a fundamental role in promoting mental health. Understanding its mechanisms, variability, and the consequences of its restriction is therefore essential, especially for animals housed in artificial environments that restrict social contact, such as in commercial farms.

This dissertation aimed to better understand physical contact in pigs; a social species that naturally lives in structured groups where social interactions are partly mediated through touch. In particular, it explored the natural variation in physical contact behaviour in pigs, and how sex, age, kinship, social dominance and environmental conditions may shape this variation. The study combined live and video-based behavioural observations of pigs. Data were analysed using mixed models, permutation tests, social network analysis, and principal component analysis. The research questions were explored across two experiments and resulted in three scientific publications.

The findings reveal that pigs express a broad repertoire of behaviours involving physical contact, which differs in function and underlying dynamics. Snout-body contact interactions were the most frequent and consistent in their occurrence from the different types of physical contact, occurring across all individuals regardless of sex, age, season, dominance status, or kinship. Social network analyses showed near-complete density and reciprocity, indicating that these interactions are equally distributed within the group. Additionally, the study showed that pigs form preferential associations, mainly based on snout-head and snout-body contact (and to a lesser extent allogrooming), which can vary in strength and can change over time, particularly following social disruptions such as temporary separation for farrowing. These results suggest that snout-head and snout-body contact play a key role in group cohesion, likely serving affiliative and recognition functions.

In contrast, snout proximity (sniffing a conspecific without making physical contact) showed different patterns, being strongly influenced by sex. Males performed this behaviour significantly more than females, independent of other factors. This may reflect its role in social assessment while avoiding direct contact, potentially linked to the higher levels of aggression typically observed in males. Supporting this interpretation, pigs showed reduced snout proximity towards kin.

Other behaviours, such as lying in contact, followed patterns similar to snout-head and snout-body contact, being expressed across individuals and seasons. While clearly linked to thermoregulation, the frequency of lying in body contact even in warmer conditions suggests an additional affiliative function. Allogrooming and social play were observed less frequently and appeared to be expressed only by specific individuals rather than being widespread group behaviours.

Overall, this dissertation highlights the complexity and functional significance of physical contact in pigs. It demonstrates that different forms of contact serve distinct roles, from maintaining group cohesion to facilitating social assessment, and that these behaviours can be differently shaped by individual or social factors, particularly sex differences. Importantly, the findings underline that physical touch represents a fundamental component of social life in pigs. From an applied perspective, this has direct implications for animal husbandry: providing opportunities for positive physical contact may improve welfare and reduce stress-related behaviours.

Streszczenie

Potrzeba kontaktu fizycznego w ostatnich latach zyskała rosnącą uwagę w badaniach wielu gatunków zwierząt, szczególnie po wprowadzeniu ograniczeń społecznych związanych z pandemią COVID-19. U gatunków społecznych kontakt fizyczny odgrywa fundamentalną rolę w promowaniu zdrowia psychicznego. Zrozumienie jego mechanizmów, zmienności oraz konsekwencji jego ograniczenia jest zatem kluczowe, zwłaszcza w przypadku zwierząt utrzymywanych w środowiskach sztucznych, które ograniczają kontakt społeczny, takich jak fermy komercyjne.

Niniejsza rozprawa doktorska ma na celu pogłębienie wiedzy na temat kontaktu fizycznego u świń, gatunku społecznego, który naturalnie żyje w uporządkowanych grupach, gdzie interakcje społeczne są częściowo mediowane przez dotyk. W szczególności badano naturalne zróżnicowanie zachowań związanych z kontaktem fizycznym u świń oraz to, w jaki sposób płeć, wiek, pokrewieństwo, dominacja społeczna i warunki środowiskowe mogą wpływać na to zróżnicowanie. W pracy zastosowano podejście integrujące obserwacje behawioralne prowadzone zarówno bezpośrednio, jak i na podstawie nagrań wideo. Zebrane dane poddano analizie z wykorzystaniem modeli mieszanych, testów permutacyjnych, narzędzi analizy sieci społecznych oraz analizy składowych głównych. Realizacja celów badawczych opierała się na dwóch eksperymentach, których wyniki zostały przedstawione w trzech publikacjach naukowych.

Wyniki pokazują, że świnie wykazują szeroki repertuar zachowań obejmujących kontakt fizyczny, który różni się funkcją i podstawową dynamiką. Interakcje kontaktu ryjem z ciałem (snout-body contact) były najczęstsze i najbardziej stałe w swojej częstości występowania spośród różnych typów kontaktu fizycznego, występując u wszystkich osobników niezależnie od płci, wieku, sezonu, statusu dominacji czy pokrewieństwa. Analizy sieci społecznych wykazały niemal pełną gęstość i wzajemność, co wskazuje, że te interakcje są równomiernie rozłożone w grupie. Dodatkowo badanie wykazało, że świnie tworzą preferencyjne powiązania, głównie oparte na kontakcie ryj–głowa i ryj–ciało (a w mniejszym stopniu na allogroomingu), które mogą różnić się siłą i zmieniać się w czasie, szczególnie po zaburzeniach społecznych, takich jak tymczasowa separacja w okresie okołoporodowym (farrowing). Wyniki te sugerują, że kontakt ryj–głowa i ryj–ciało odgrywają kluczową rolę w spójności grupy, prawdopodobnie pełniąc funkcje afiliacyjne i rozpoznawcze.

W przeciwieństwie do tego, bliskość ryja (snout proximity – wąchanie osobnika bez kontaktu fizycznego) wykazywała inne wzorce, będąc silnie zależna od płci. Samce wykonywały to zachowanie istotnie częściej niż samice, niezależnie od innych czynników. Może to odzwierciedlać jego rolę w ocenie społecznej przy jednoczesnym unikaniu bezpośredniego kontaktu, potencjalnie powiązaną z wyższym poziomem agresji typowo obserwowanym u samców. Potwierdzając tę interpretację, świnie wykazywały zmniejszoną bliskość ryja wobec krewnych.

Pozostałe zachowania, takie jak leżenie w kontakcie, wykazywały wzorce podobne do kontaktów ryj–głowa i ryj–ciało, występując u wszystkich osobników oraz w różnych porach roku. Choć zachowanie to jest wyraźnie związane z termoregulacją, jego utrzymywanie się z wysoką częstością także w cieplejszych warunkach sugeruje dodatkową funkcję afiliacyjną. Allogrooming oraz zabawa społeczna obserwowano rzadziej i wydają się występować jedynie u wybranych osobników, a nie jako powszechne zachowania na poziomie całej grupy.

Niniejsza rozprawa podkreśla złożoność oraz funkcjonalne znaczenie kontaktu fizycznego u świń. Wykazuje, że różne jego formy pełnią odmienne role od utrzymywania spójności grupy po ułatwianie oceny społecznej – oraz że zachowania te mogą być kształtowane przez czynniki indywidualne i społeczne, w szczególności przez różnice płciowe. Co istotne, wyniki wskazują, że dotyk stanowi podstawowy element życia społecznego świń. Z perspektywy aplikacyjnej ma to bezpośrednie implikacje dla hodowli zwierząt: zapewnienie możliwości pozytywnego kontaktu fizycznego może przyczyniać się do poprawy dobrostanu, ograniczenia zachowań związanych ze stresem oraz poprawy wyników rozrodu.

1 Introduction

Physical contact is the most direct experience of interaction with our physical and social environment (Farroni et al., 2022) and is crucial for many aspects of the health and welfare of group-living species (Cascio et al., 2019; Jablonski, 2021; Thomas and Kim, 2021), including humans (Packheiser et al., 2024). Social touch, which refers to gentle physical contact, stimulates C-tactile afferent nerve receptors (Walker et al., 2017). These fibres respond preferentially to gentle and slow stroking (Cascio et al., 2019) and are indicated as mediators of oxytocin. The study of physical touch and its effects on health is of primary importance. This is particularly evident in the context of the COVID-19 pandemic, during which social restrictions resulted in reduced physical contact (Packheiser et al., 2024). During the pandemic, a majority of individuals were confined to their homes for extended periods, resulting in a substantial reduction in social interactions, in particular those involving skin-to-skin contact (i.e., social touch). Social distancing restrictions during the COVID-19 pandemic have been associated with higher anxiety, loneliness, depression, and stress, as well as declines in mood (Von Mohr et al., 2021; Grandi & Bruni, 2024). Social touch was identified as the most desired form of touch during this period (Von Mohr et al., 2021). Notably, the effects of social touch on mental health appear to be particularly pronounced in humans with clinical disorders (Packheiser et al., 2024).

A similar dynamic is observed in animals in commercial farming systems. Housing conditions in these systems often limit both physical contact and other forms of social interaction. Restrictions are mostly imposed for management reasons, and include factors such as space availability (cattle: Miller and Wood-Gush, 1991), pen design (pigs: Andersen et al., 1999), group size (sheep: Jørgensen et al., 2009) and social instability (goats: Andersen et al., 2008). Under restricted space allowance, animals may have limited choice regarding whom to be in contact with and may be forced to be in physical contact. This could potentially lead to social stress and conflict, as subordinate animals may be unable to distance themselves from dominant ones (Arey and Edwards, 1998). At the same time, social species that are kept in social isolation, such as single housed calves (Chua et al., 2002; Vieira et al., 2010) and sows in gestation crates (Jarvis et al., 2006; Yin et al., 2016), may suffer from the lack of physical contact. Although in many cases solitary housing still maintains some degree of contact with conspecifics (e.g. visual, auditory, and olfactory cues), the lack of physical

contact specifically still induces a stress response in social species (pigs: Herskin & Jensen, 2000).

In this dissertation, domestic pigs (*Sus scrofa domesticus*) were studied, as they are a relevant model species for human biomedical research but are also an important livestock species (Meurens et al., 2012; Swindle et al., 2012). Domestic pigs live in social groups, where they frequently exhibit affiliative behaviours, consequently responding strongly to social isolation, with consequences for their behaviour and neurobiology (Ruis et al., 2001; Herskin and Jensen, 2000). Pigs have a wide repertoire of behaviours based on physical contact, including allogrooming (Meynhardt, 1982), resting in body contact (Newberry and Swanson, 2001), social play (Brown et al., 2015; Horback, 2023; Steinerová et al., 2024) and snout contact (Camerlink and Turner 2013; Khatiwada et al., 2025a). Pigs rest frequently in body contact (Ekkel et al., 2003; Camerlink et al., 2022a), especially at a young age, which helps them to remain in their thermal comfort zone (Herpin et al., 2002; Huynh et al., 2005). At higher temperatures, when thermoregulation is less essential for their survival, they are more likely to space apart (Huynh et al., 2005). They also make frequent snout contact, which serves various purposes such as affiliation, recognition (Camerlink and Turner, 2013) and mother-offspring bonding (Petersen et al., 1990; Stanged and Jensen, 1991). Initial work on social nosing (i.e., the full repertoire of snout related social interactions) showed that pigs which received more social nosing had a higher growth rate (Camerlink et al., 2012), suggesting a beneficial effect of snout contact. Allogrooming does occur in pigs but has rarely been studied (mostly in wild boar: Meynhardt, 1982), and the studies which were conducted in juvenile domestic pigs showed that allogrooming occurred infrequently (Goumon et al., 2020; Camerlink et al., 2022a).

To better understand the mechanisms underlying physical contact, it is essential to identify how individual factors contribute to the expression of these behaviours. Two studies on groups of growing pigs reported that sex, dominance status and genetic relatedness were only partially related to affiliative behaviours (Goumon et al., 2020; Clouard et al., 2024). However, other studies have shown that there is an effect of dominance status on spatial proximity in pigs, with dominant pigs often spacing further away from others, eventually resulting in less social interactions initiated (McCort and Graves, 1982). Sex differences have also been reported in social nosing interactions among piglets (Clouard et al., 2022) and growing pigs (Khatiwada et al., 2025b). Further, familiarity might influence the expression of

a range of social behaviours, with familiar pigs nearly twice as likely to engage in snout-body, snout-head and snout-snout contacts (Jowett et al., 2025).

The aim of this study was to explore and increase our understanding of the significance of physical contact. Specifically, to explore the natural variation in physical contact behaviour in pigs, and how sex, age, kinship, social dominance and environmental conditions may shape this variation. This study can contribute to the improvement of welfare in commercial farms. It does so by considering social tendencies and needs, aligning management practices more closely with behavioural biology to promote healthier livestock populations. In addition, given the relevance of pigs as a model for human research, these findings may have implications for other research fields, highlighting the importance of social relationships and supporting improved housing conditions for research animals.

2 Hypotheses

1. The frequency of affiliative contact, such as snout contact and allogrooming, remains stable throughout the year due to its importance in social cohesion (publication 1).
2. Pigs show stable social preferences across time and social networks with high levels of reciprocity and density, indicating strong group cohesion (publication 2).
3. Physical contact occurs more frequently between genetically related pigs than non-genetically related ones, in females than in males, and in subordinate rather than dominant pigs (publication 3).

3 Objectives

1. To explore the natural variation in physical contact behaviour (publication 1).
2. To determine whether domestic pigs form long-term affiliative social preferences and if their number and stability relate to group-level sociability (publication 2).
3. To investigate how sex, age, kinship, social dominance and environmental conditions may shape this variation (publication 3).

4 Material and methods

The dissertation includes the experimental procedures from three different experiments. Experiment 1 resulted in Publication 1 and 2 and was based on data collected in 2022-2023 at the pig research facilities of IGBZ PAN, Jastrzebiec, Poland. Experiment 2 resulted in publication 3 and it was based on data collected in 2024-2025 at the Easter Howgate pig unit of Scotland's Rural College (SRUC), in Easter Howgate, the UK. The experiment was approved by the Animal Ethics Committee (VERC) of SRUC and was part of a larger experiment authorised by the UK Home Office (Project license P3850A80D/PP1403242). The experimental work was approved by the Local Ethics Committee of Warsaw (LKE 2), Poland, with protocol number WAW2/111/2023. The animal and housing section is reported separately for each experiment.

4.1 Animals, housing and social treatments

4.1.1 Experiment 1

A herd of ten sub-adult females pigs (*Sus scrofa domesticus*) of the native Polish Puławska breed were studied at the pig research farm of the Institute of Genetics and Animal Biotechnology of the Polish Academy of Science, Warsaw, Poland. The group consisted of seven full-sibs from one litter, two full sibs from another litter and one half-sib. They originated from the same breeder, where the gilts were in the same group from weaning to 50 kg and thereafter split into smaller groups. From arrival at the research facilities (3 months prior to the study) they were kept as one group, under the same conditions and management as during the study. At the onset of the study, pigs were eight months old and had an average weight of 106 kg (range 80 – 128 kg), whereas they were 15 months old and approximately double the weight at the end of observations. Since their arrival at the facility, pigs were housed in a barn with natural ventilation and no source of heating. The Puławska breed is well adapted to the colder climate (Babicz et al., 2020) and therefore is well-suited to be kept at lower temperatures than in commercial farms. The group was kept in an indoor pen of 16 m × 7 m (movement area of 108 m^2), which guaranteed an area of 10.8 m^2 per pig, whereas the minimum required by EU Council Directive 2008/120/EC is at least 1.64 m^2 per gilt and 2.25 m^2 per sow. The pen had a concrete floor with straw bedding (ca. one 500 kg straw bale). The bedding was changed once a week during autumn, winter and spring, and twice a week during summer, in order to always keep at least ca. 500 kg of bedding straw on the floor. Additionally, the pigs were provided with ca. 10 kg of fresh straw ca. 30 min. before

the start of the observations, in order to keep the bedding area clean. From winter onwards, a covered hut (dimensions: 6.0 ×2.0 ×1.5 m; 1.2 m^2 / pig) made from wood was provided within the barn for the pigs to stay warm. Pigs were floor fed twice daily (at 9 am and 3 pm) by spreading the food in a line across the floor. Feed was a commercial fine-ground sow meal (10.26 MJ/kg; 16 kg feed when dry for the whole group) which was mixed with water and ca. 150 ml rapeseed oil. The same feed type and quantity was provided throughout the year. Water was available ad libitum from two drinkers. The building had natural daylight and artificial lights were on from 07:00–18:00 h, which together provided an illumination of 77–80 lux during daylight hours. The ambient temperature was recorded with two thermometers (Xiaomi Mi temperature and humidity monitor 2) for the daily average, and by a data logger (Eliotech RC-5). One thermometer and the data logger were placed just outside the pen enclosure, while the second thermometer was placed inside the hut.

4.1.2 Experiment 2

Sixteen groups of domestic pigs (Large White × Landrace sows × American Hampshire boars) were studied in the Easter Howgate Pig Research Unit in August 2024 to March 2025. A total of 212 pigs (n=108 entire males and n=104 females) from three farrowing batches were observed for dominance rank. Each batch was observed in a different month. From these, 96 pigs (47 males and 49 females) were further observed as focal animals. Cross-fostering was kept to a minimum and done only for litters with more than 10 piglets and where the sow had a body condition below the herd average. Pigs were weaned at 4 weeks and regrouped into single-sex groups. At 8 weeks of age, pigs were regrouped into new single sex groups of 10-16 individuals each. While mixing events are known to influence social behaviour in pigs (Petherick and Blackshaw, 1987), all individuals experienced the same mixing history, allowing behavioural variation to be examined under comparable social conditions. The study started after this second event of mixing at 8 weeks of age and finished at 12 weeks of age. Pigs were grouped by similar weight and siblings were divided over as many pens as possible, whilst ensuring that each pig had at least one sibling and one pig from the same weaning pen in their new group. Female pigs were housed in pens that previously housed males and vice versa, so that no pig remained in its original pen, to avoid an effect of home pen territory on aggression. The groups were housed in enriched conditions with a floor space of 6.9 m × 2.1 m (14.49 m^2; 1.45 - 0.91 m^2 / pig). Straw was provided as bedding

material, with dirty straw removed and fresh straw added as necessary each day. One Porcichew toy (Ketchum manufacturing company, UK) and one length of Manilla rope (Westward Rope and Wire, UK) hung from the pen wall were provided as enrichment objects. Shed temperature was adjusted to the age of pigs and controlled automatically. Food and water were provided ad libitum. Pigs were individually recognized by their ear tag and by a spray mark applied on their back with animal marker spray (East Riding Farm Services, UK). The back mark for identification was redone twice a week, in the morning, at least one hour before starting the observations. Daily checks were done to evaluate pigs' health.

4.2 Experimental procedures

4.2.1 Behavioural observations (Experiment 1)

For Experiment 1, behavioural observations were conducted across four seasons within one twelve-month period (autumn and winter 2022, spring and summer 2023). Behaviour was observed day and night. Across the year, four to five females per season were pregnant (four in autumn and winter, and five in spring and summer), which was accounted for in the statistical analysis. Due to their pregnancies, six out of ten gilts were temporarily relocated (outside the group) for farrowing in between two observation blocks and returned to the group at least one week before the next observation block. As the group was stable from a young age, and pigs were mostly sisters, the disruption of reintroducing pigs subsided within the course of a few days. The observations included 10 or 9 pigs in each season. Studying a small group of animals allowed us to obtain more detailed and longitudinal data that would not have been possible with a large number of animals, and thus better suited our current aim to investigate cross-seasonal and diurnal patterns in natural contact behaviour in detail.

One person conducted continuous behavioural observations, using the ethogram in Table 1 while noting the actor and recipient of each behaviour. Only active lying down was scored (Goumon et al., 2020), which means that contact behaviour was only scored for the actor, i.e., the animal that was actively making the movement of lying down beside another pig, whereas the recipient who was already lying was not additionally recorded as lying in contact. In publication 2, only nosing body, nosing head and allogrooming from the ethogram in Table 1 were scored.

Behavioural observations were conducted using the Animal Behaviour Pro App, version 1.2 (University of Kent, Canterbury, UK), installed on an iPad. Pigs were marked for individual identification with animal marking crayon (Raidex crayon, red or yellow) on their back every day, and marking was completed at least 30 min before the start of the observations. Additionally, pigs were recognized by their individual coat patterns. Daytime observations took place between 09.30 and 18:00 h and were scheduled into blocks of 2 or 2.5 h, with a maximum of 5 hours (2 observation blocks) a day. The timing of the observation blocks was balanced across the observation days. Daytime observations were conducted live, except for some days during the winter season. The observer positioned himself stationary outside the pen, largely out of sight of the pigs, and did not interact with them. Night time observations were recorded on sports cameras (AKASO EK7000), one in the main area and one inside the hut, and lasted from 18:30–06:30 h (12 h). Night time observations were obtained from five night recordings balanced across the observation weeks. Four orange LED light tubes (126 cm length) were used to guarantee visibility, providing an illumination of 25–30 lux, but were sufficiently dim to prevent disturbance to the pigs during night observations. In each season, 101.5 hours of observations (41.5 h daytime and 60 h nighttime) were carried out across ten days within a two-week time frame. All behaviours were scored as frequencies while for lying in body contact and other body contact (see ethogram) the duration was also recorded.

Table 1. Ethogram of behaviours scored live and from video.

Behaviour	**Description**
Social behaviour (frequency)	
Aggression	Bites while the snout contacts the skin of another pig, resulting in potential skin damage; includes reciprocal fights.
Agonistic behaviour	Displacing another individual from a resource (with or without physical contact), head knocks, directing an open-mouth bite to the other without making physical contact, chasing the other without bites that make physical contact.
Allogrooming	Gently nibbles or licks the body or head of another pig; does not cause acute skin damage to the other pig.
Belly nosing	Repetitive and slightly forceful up and down snout movement on the belly of another pig.
Mounting	Place both forelegs on the body of another standing or lying pig.

Nosing body	Touches the body of another pig with its nose disc, excluding the head.
Nosing head	Touches another pig's head with its nose disc; can include the snout; excludes allogrooming.
Nudging	Gives a short non-forceful push to another pig (any part of the body) with its snout.
Resting behaviour (frequency and duration)	
Full body contact* (Fig.1)	Lying with a minimum of approximately 75% of its body against its neighbour.
Partial body contact* (Fig.1)	Lying with approximately 25 – 74% of its body against its neighbour.
Extremities contact* (Fig.1)	Lying with approximately 1 – 24% of its body against its neighbour; includes contact of only the snout, legs, tail or other small portion of the body.

* For these behaviours the orientation (parallel head-to-head, parallel head-to-tail, or nonparallel) was scored as a modifier

Figure 1. Photos illustrating the different lying orientations (parallel head-to-head, parallel head-to-tail and nonparallel) during resting in full, partial and extremities contact.

4.2.2. Behavioural observations (Experiment 2)

In experiment 2 (conducted in the UK), behavioural observations were the primary form of data collection. In the first week of behavioural observations (after regrouping, at 8 weeks of age), only agonistic behaviours were scored with the aim to calculate dominance relationships. In particular, submissive behaviour was scored to assess who lost the encounter. Submissive behaviour was scored as withdrawal during an agonistic encounter, including a head-tilt-retreat, whereby the losing pig lowers its head and turns it rapidly sideways (Jensen, 1980), thereby turning the shoulder away from the opponent and refraining from retaliation for at least 10 seconds (Camerlink et al., 2016). Agonistic interactions where it was unclear whether a head-tilt-retreat had occurred were recorded as inconclusive. Pigs were observed by continuous observations for a total of 5 hours per pen through live and

video recordings between 9:00 and 16:00 h. Subsequently, a dominance score was determined for each individual using Glicko rating from the agonistic interactions with a clear outcome. Glicko rating is a system for establishing which individual is dominant based on the outcomes of their fights. The system assigns a greater increase in score to an individual when it defeats a highly successful individual than a less successful individual. It incorporates a rating value and a rating deviation (RD), which quantifies the certainty of the rating (Glickman, 1999). The model is particularly well-suited for datasets with varying numbers of interactions per individual and allowed us to determine a dominance rank from the individual scores. Glicko ratings were calculated in R software version 4.5.1 (R Core Team, 2025), using the "PlayerRatings" package (Stephenson and Sonas, 2020). After the analysis, each pig had a final rating value and a final RD based firstly on the number of victories and defeats, and also on the relative dominance exhibited during each interaction. The final ranking was determined by both the rating value and the associated RD, reflecting not only performance outcomes but also the confidence in those estimates. Default values were set at 2200 for the rating and 300 for the RD.

Based on the Glicko ratings, six focal pigs were selected per group. For each group, two pigs with the highest, the middle and lowest ranks based on their Glicko scores were selected for further observations. The rating deviation (RD) was not used in the selection of focal pigs. This resulted in 96 pigs (males and females). Observing 6 focal pigs instead of 10-16 allowed for more manageable and thus more detailed observations, leading to more accurate and reliable results. Additionally, by selecting from across the dominance hierarchy, a balanced representation within each group was maintained. The focal animals were observed in weeks 10 and 11 using the ethogram described in Table 2, using continuous observations. All interactions were scored as single events and attributed to one actor, meaning that in case of repeated events in a short time every contact was scored. For each interaction, the actor was defined as the individual that initiated the behaviour, regardless of whether the recipient was a focal or non-focal pig. Interactions between two focal pigs were recorded once, attributed only to the initiating individual. In case of behaviours that could appear symmetrical, the actor was identified as the pig that initiated the approach leading to the interaction. If no clear initiator could be identified, the interaction was not scored. Pigs were observed for 10 days over two weeks, 5 days a week, for a total of 10 hours of continuous observation per pen, resulting in 160 hours in total. All observations were performed using the Animal Behaviour Pro App, version 1.2 (University of Kent, Canterbury, UK), installed on an iPad.

Table 2. Ethogram for observed behaviours in 96 growing pigs of 10-11 weeks of age (experiment 2).

Behaviour	Description
Snout-snout contact	Touches another pig's snout with its nose disc; includes the nose disc of the recipient
Snout-snout proximity	A pig extends its snout in direction of the snout of another pig snout at approximately <30 cm distance without making contact
Snout-head contact	Touches another pig's head with its nose disc; excludes the snout and allogrooming
Snout-head proximity	A pig extends its snout in the direction of the head of another pig at <30 cm distance without making contact; excludes snout
Snout-body contact	Touches the body of another pig with its nose disc, excluding the head
Allogrooming	Gently nibbles or licks the body or head of another pig; does not cause acute skin damage to the other pig
Lying in body contact head-to-head	Focal pig actively lies down with its body in contact with a conspecific in a parallel orientation with their heads adjacent to or touching
Lying in body contact any other orientation	Focal pig actively lies down with its body in contact with a conspecific in a parallel head-to-tail, or non-parallel orientation
Social play	A playful interaction characterised by one or more of the following behaviours: running (incl. chasing), hopping, flopping, tossing, pushing or nudging without delivering or receiving potentially damaging aggression. It involves at least one other individual besides the actor.

5 Statistical analysis

Statistical analyses were performed in the statistical programs SAS (version 9.4, publication 1) and R (publication 2: R version 4.3.2; publications 3: R version 4.5.1), and social network analyses and social preferences were analysed using UCINET (version 6, publication 2). P-values <0.05 were considered significant whereas p-values >0.05 but <0.10 were reported as tendencies.

5.1 Mixed models

5.1.1 Contact behaviours

In publication 1, two datasets were formed for the analysis of the natural variation in physical contact behaviours over time. Dataset 1 contained the behavioural data per sow, averaged by season (no repeated observations), which was used to investigate correlations between specific behaviours. Due to the variables not being normally distributed, Spearman correlations were used. In dataset 2, behavioural data were summed per animal by time of day (day or night) and season (4 seasons), resulting in eight data lines (i.e., repeated observations) per individual. The durations and the frequencies were converted to 12-hour averages, so that the behaviours during the day and night were both expressed as average per 12 hour time block. Durations (initially in seconds) were converted to minutes. Behaviours were analysed using mixed models (MIXED Procedure) with a Gaussian distribution. The response variable was the behaviour, and the predictor variables were season (4 seasons), daytime (day / night), their interaction (season × daytime) and whether the females were pregnant or not. When pregnancy did not significantly influence the response variable it was removed from the model. The animal ID was entered as a random statement to account for repeated observations per animal (10 subjects, 8 observations per subject). As the model was used multiple times (for each behaviour), we corrected for multiple testing using the Bonferroni adjustment. Behaviours for which the model residuals did not follow a normal distribution (also not after transformation) due to infrequent occurrence were reported descriptively.

5.1.2 Effect of individual traits on sociability

In publication 3 (experiment 2), to investigate the individual factors that can influence contact behaviour, observations were made on contact, spatial proximity and social behaviour. As these behaviours may correlate, we explored whether the measured variables would fall into certain correlated categories. For this, a Principal Component Analysis (PCA) was conducted, which is described in section 5.4. The resulting 3 Principal Components were analysed in mixed models. Using mixed models with the Principal Component as the response variables, we assessed the influence of dominance rank, sex, and kinship on the expression of each component. To do so, we extracted the PC scores for each individual across all three components. These scores were then used as response variables in linear mixed models, using the lmer function from the “lme4” package in R (Bates et al., 2015). Sex (male vs. female),

dominance score (high, mid, low), and kinship-based interactions (proportion) were included as fixed effects. Variables pen and batch, which also accounted for seasonal fluctuations, were added as random effects. Model assumptions were assessed by inspecting the residuals. Histograms and QQ-plots indicated approximate normality, and residuals versus fitted values plots confirmed homoscedasticity. Multicollinearity among fixed effects was evaluated using variance inflation factors (VIFs), with all VIFs well below 5 (dominance: 1.00, kinship-based interactions: 1.01, sex: 1.00), indicating no collinearity among fixed effects. P-values <0.05 were considered significant. For the kinship-based interactions, because the number of siblings varied between groups, as well as the total number of group members, we corrected kin interaction rates according to the opportunity pigs had of interacting with a sibling. For each focal pig and behaviour, we calculated an adjusted kinship proportion, defined as kinship proportion per group = (n interactions kin / total) / (n siblings / total n -1). This formula calculates whether individuals interacted with kin more or less than expected based on availability, and is derived from the simple ratio index from Whitehead and James (2015). Values > 1 indicate a bias toward kin, values of 1 indicate interactions proportional to availability, and values < 1 indicate kin avoidance. Graphs were made with the "ggplot" package (Wickham, 2016).

5.2 Social network analysis

To better understand the social dynamics within groups, social networks and social preferences analysis were performed (publication 2). SNA is a method to assess the structure of relationships in a social group. This approach examines individuals and groups in the context of interactions (called 'ties' or 'edges') between group members (represented as 'nodes') (Wey et al., 2008). SNA allows the study of how social relationships change over time, thus providing insights into the stability and dynamics of social groups. This can be particularly important for understanding how pigs form and maintain social bonds. In this study, we analyzed how the social network of affiliative behaviours (snout-body, snout-head and allogrooming; Table 1) evolves over time by looking at changes in network properties using the measures of density, reciprocity and degree centrality. These measures allow evaluation of the stability, cohesion and sociality of the group over a long period of time. Stable social networks tend to have consistent density, high reciprocity, and stable centrality measures. Here, we used SNA to verify if these measures relate to the social preferences and how these change in the long term.

Density is a measure of how well individuals are connected within a group and facilitates the examination of changes over time within the same group of animals across different periods (Büttner et al., 2020). Density is the ratio between the number of actual observed connections and the number of potential connections given a group of individuals of the same size. The value ranges from 0 to 1, whereby 1 indicates that all potential connections were actually observed (i.e., every animal interacted with every other animal).

Reciprocity refers to the proportion of connections within the network that were reciprocal rather than uni-directional. Reciprocity is a crucial aspect of a social structure, as it can refer to both the balance and the hierarchy of a network. A network composed predominantly of reciprocal affiliative connections shows greater stability than one composed mostly of non-reciprocal connections (Hanneman and Riddle, 2005). Reciprocity has a value between 0 and 1 and represents the proportion of dyads in which the behaviour flowed in both directions relative to the total number of dyads in the group. This value will be 0 if none of the connections are mutual and 1 if all connections are mutual.

Degree is a measure of the centrality of an individual and quantifies the number of group members an individual interacted with (Farine and Whitehead, 2015). Additionally, the disparity in degree between group members can be quantified as a group-level metric, termed degree centralization. *In-degree centralization* is a group-level measure and quantifies the extent to which a single individual is the primary recipient of interactions in the group, whereas *out-degree centralization* measures the extent to which an individual is the primary initiator of interactions. Hence, in- and out-degree centralization reflect the heterogeneity in sociability within the group. It ranges from 0 (maximum homogeneity) to 1 (maximum heterogeneity). As this study focused on the nature and stability of the social network over a relatively long period of time, we calculated measures at group level (density, reciprocity, in- and out-degree centralization) across the four seasons to observe their trends. Stable networks would likely exhibit relatively smooth and predictable temporal dynamics. For social network analysis we created a matrix of interactions for each season, where the columns and lines represented individual subjects, and the intersections of the lines with the columns represented the frequency of interactions between those two individuals. Frequencies of snout-body contact, snout-head contact and allogrooming (Table 1), as well as during day and night, were summed, resulting in one matrix for each season. We then calculated density, reciprocity, out-degree centralization and in-degree centralization using the Whole-Network measures function in UCINET software (version 6 for Windows) (Borgatti et al., 2002).

5.3 Social preferences

In publication 2, social preferences of each pig in each season were scored using the same matrices of interaction used for the SNA analysis described above. All the statistical analyses were conducted in UCINET (version 6) or R (version 4.3.2). To evaluate whether the frequencies of affiliative interactions were more variable between individuals than expected by chance, we conducted a Monte Carlo test for the interaction rates matrix of each season (following Goumon et al., 2020). The Monte Carlo method is a computational technique that uses random sampling to obtain numerical results. In this study, the Monte Carlo method created a theoretical distribution of means and CVs of interaction rates by permuting the data 1000 times. We considered that social preferences were likely to exist when the CV of the observed interaction data was higher than the mean CV of all permuted replicates. In this case, a high CV would indicate high heterogeneity in the interaction rate. Significance was established when the observed CV was outside the 95 % confidence interval of the distribution of CVs created by the Monte Carlo test. Subsequently, preferential associations were analyzed by using frequency matrices. The half-weight association index (HWI: Cairns and Schwager, 1987, Ginsberg and Young, 1992) was calculated with the equation: HWI $=x/(na+nb)/2$; where x is the number of times individual a and individual b interacted with each other in the observation period; na is the number of individual a interactions in the same period; and nb is the number of individual b interactions in the same period. The HWI quantifies the strength of association between pairs of individuals based on their interaction frequencies, taking into account both the number of times two individuals interact with each other and the number of times they interact with other individuals. Social preferences were classified based on the average HWI as a threshold value. Preferences were classified as strong when the value obtained was greater than twice the average HWI; weak when it was equal to or lower than twice the average HWI; and classified as no association when the value was lower than the average HWI. This threshold value was chosen because it is approximately twice the expected value than if associations were completely random, and has been used previously in similar studies (as in Durrell et al., 2004, Gero et al., 2005, Li et al., 2018, Goumon et al., 2020). For each season, a matrix of HWI was created. The rows and columns of the matrix represented individual pigs, and the cells contained the HWI values between the pigs corresponding to the respective row and column. We then correlated the four matrices to evaluate repeatability of association strength using the Quadratic Assignment Procedure (QAP) with 5000 permutations. QAP is a measure of correlation and, with this

test, we evaluated whether preferential associations repeated across the four seasons. The number of permutations was based on Li et al. (2018) and corresponds to the UCINET default setting, which balances robust significance testing with computational efficiency. Correlations were based on the overlapping dyads present in both matrices.

5.4 Principal component analysis

Principal component analysis (PCA) was run in publication 3 to identify behavioural profiles. This approach reduces data dimensionality by transforming the original variables into a new set of uncorrelated variables (principal components, PCs) that capture most of the dataset's variance (Abdi and Williams, 2010). Each PC is characterized by a set of co-occurring behaviours and can therefore be interpreted as a behavioural profile. Individual PC scores reflect the extent to which each animal expressed that profile. All behavioural variables (frequencies of snout-snout contact or proximity, snout-head contact or proximity, snout-body contact, allogrooming, lying in contact head-to-head or any other orientation, social play; Table 2) were available for all focal individuals. Zero values reflected the absence of a behaviour during the observation period rather than missing observations; therefore, no data removal or imputation was required prior to the PCA. Before extracting the principal components, the data were standardized (argument scale = TRUE in the prcomp function) using z-transformation (mean = 0, SD = 1) and inspected for outliers using boxplots, with observations identified as outliers if they had a z-value greater than 3, following Tabachnick et al. (2007). A small number of outliers was identified (12 data points out of 864 behavioural measurements across 11 individuals); however, sensitivity analyses excluding these individuals produced a comparable PCA structure. Results from the full dataset were therefore considered. We then assessed the suitability of the dataset for PCA analysis. Pearson correlations were calculated between all z-transformed variables. The Kaiser-Meyer-Olkin measure of sampling adequacy was 0.73, and Bartlett's test of sphericity was significant ($\chi^2 = 171.86$, $p < 0.001$), indicating that the correlation structure of the behavioural variables was suitable for PCA. We performed a PCA with orthogonal rotation using the prcomp function from the "stats" package to run the analysis. We used the "factoextra" package (Kassambara and Mundt, 2016) to visualize the results with graphs. Once all principal components were extracted, only those with eigenvalues exceeding 1 were retained for further analysis, following the Kaiser criterion (Kaiser, 1960).

6 Results

6.1 Lying in body contact (Publication 1)

We predicted that pigs would vary frequency of body contact in relation to thermoregulatory needs. Pigs spent on average 40 ±9% (SD) of the observed time in body contact, which was mostly lying with their extremities in contact (71 ±4%, SD), followed by lying in partial body contact (16 ±5%, SD) or full body contact (13 ±7%, SD) and frequently showed contact behaviours, of which the most frequent was nosing the head and body. The frequency and duration of lying in partial body contact differed between the seasons ($p < 0.001$), in which autumn had significantly higher average values between day and night (71 min; 2.7 times) than winter (31 min; 0.84 times) and summer (14 min; 0.5 times) but did not significantly differ from spring (56 min; 1.08 times) (Fig. 2a). In summer, when the temperature was highest, the duration of lying in partial body contact was significantly lower than in other seasons, whereas the duration of lying in full body contact tended to be lower ($p = 0.06$) (Fig. 2a). At the same time, in summer, the duration of lying with extremities in contact tended to be higher ($p = 0.06$) (Fig. 2a). Pigs spent more time lying in body contact during the night (340 min out of 12 hours) than during the day (211 min) (for all 3 behaviours $p < 0.01$; Fig. 2a). There was a season by daytime interaction for partial body contact ($p = 0.04$), with autumn day differing from summer and winter day, and autumn night from summer and winter night. Spring day differed from spring night, but only spring night differed from both summer day and summer night time and also from winter daytime.

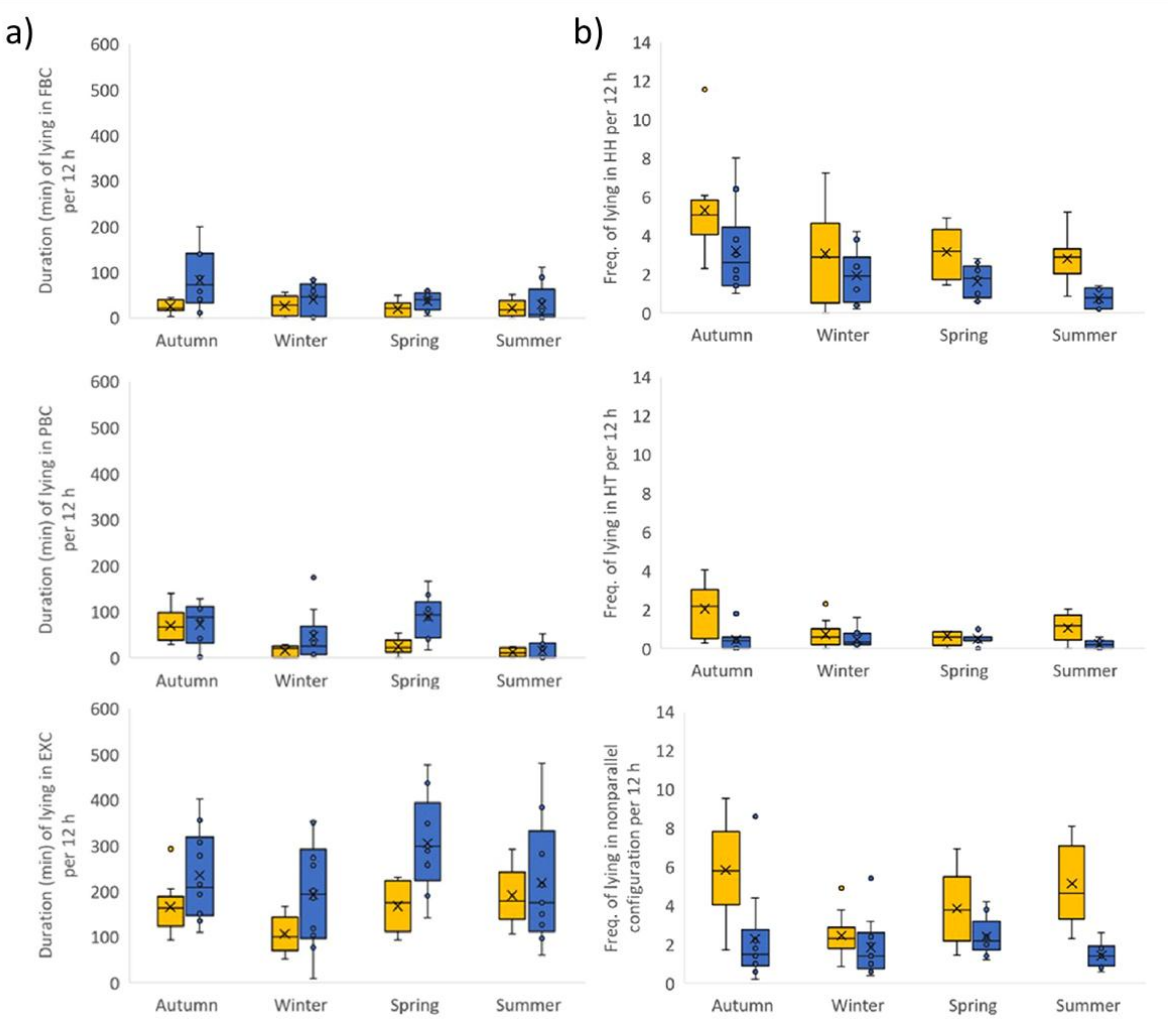

Figure 2. a) Boxplots of duration in minutes per 12 h time block, by season and day (in yellow) and night (in blue), for lying in full body contact (FBC), partial body contact (PBC), and with extremities in contact (EXC). Boxes range from 1st-3rd quartile while the inner line represents the median and the X the average. Whiskers below and above the boxes show the minimum observation above the lower fence (Q1 - 1.5 IQR) and the maximum observation below the upper fence (Q3 + 1.5 IQR). Outliers are represented as solid circles. **b)** Boxplot of frequencies of lying head-to-head (HH), head-to-tail (HT) and nonparallel per 12 h time block, by season and daytime (day: yellow; night: blue). Boxes range from 1st-3rd quartile while the inner line represents the median and the X the average. Whiskers below and above the boxes show the minimum observation above the lower fence (Q1 - 1.5 IQR) and the maximum observation below the upper fence (Q3 + 1.5 IQR). Outliers are represented as solid circles.

Pigs mostly lay in nonparallel orientation (133 ± 88 min, SD; 3.2 ± 1.89 times on average per 12 h; 48 % of observations) or head-to-head (118 ± 41 min, SD; 2.8 ± 0.87 times; 43 % of observations), but clearly least in the head-to-tail orientation (24 ± min 15, SD; 0.8 ± 0.41

667 times; 9 % of observations). Season did not influence the percentage (based on durations) of
668 lying nonparallel (p=0.08), head-to-head (p = 0.20) or head-to-tail (p = 0.52). The three lying
669 orientations occurred with similar frequency during the day and night (p >0.05). There was a
670 season by daytime interaction for lying head-to-head (p = 0.008), but with the Bonferroni
671 correction this did not result in significant post-hoc differences. Interestingly, pregnant pigs
672 were lying less in head-to-tail orientation (pregnant: 5.7 ± 1.65 min; not pregnant: 11.3 ± 1.57
673 min; p = 0.03). The frequency of lying orientations, which reflects the number of times pigs
674 get up and lie down again from a certain lying orientation, showed a different pattern as
675 compared to the percentages based on the durations. Season influenced the frequency of lying
676 head-to-head (p = 0.001) and head-to-tail (p = 0.01) but not lying nonparallel (p = 0.06), with
677 the frequency of lying down in a head-to-head and head-to-tail orientation being greater in
678 autumn as compared to the other seasons (Fig. 2b). The frequency was always greater during
679 the day than during the night (all p <0.001). There was a season by daytime interaction for
680 the frequency of lying down head-to-tail (p = 0.01), whereby autumn day differed from all
681 other time points except summer day. There was also an interaction for nonparallel
682 orientation (p = 0.002), whereby autumn day differed from all other time points except spring
683 and summer daytime; autumn night differed from summer day; and summer day differed
684 from summer night and winter night (Fig. 2b). Similar to the duration, pregnant pigs were
685 lying less frequently head-to-tail (pregnant: 0.55 ± 0.125 times; not pregnant: 0.97 ± 0.119
686 times; p = 0.03).

687 ## 6.2 Frequency of affiliative contact (Publication 1)

688 Nosing body and nosing head occurred equally across the seasons (p = 0.33; p = 0.94,
689 respectively). During the daytime, sows nosed each other's body on average 5.7 ± 0.63 times
690 and heads 7.3 ± 0.50 times per 12 h, but hardly showed these behaviours during the night
691 (nosing body: 0.4 ± 0.63; nosing head: 0.8 ± 0.50 times per 12 h) (both p <0.001). Nosing
692 body and nosing head showed no interaction between season and time of day (p = 0.32; p =
693 0.88, respectively). Nosing body, but not nosing head (p >0.05), was shown significantly
694 more by sows who were not pregnant (pregnant: 1.7 ± 0.69 times per 12 h; not pregnant: 4.3
695 ± 0.66 times per 12 h; p = 0.02). Allogrooming, mounting, nudging and belly nosing occurred
696 infrequently and mostly by specific individuals. Allogrooming was shown by two pigs, of
697 which one showed substantially more allogrooming (in total 40 out of 58 times shown by the
698 same pig). Allogrooming correlated with nosing body, nosing head and nudging, but not with
699 mounting (Table 3). Mounting was shown only by 4 individuals (24 times in total) and

correlated with nosing body, nosing head and nudging. Nudging, which occurred 160 times in total, correlated with nosing body and mounting, and not with nosing head (Table 3). The sum of mounting and nudging, reflecting sexual behaviour, was significantly less in pregnant females (pregnant: 0.15 ± 0.255 times per 12 h; not pregnant: 1.0 ± 0.242 times; p = 0.02). Belly nosing, expressed in the same manner as seen in young pigs, did also occur in the sub-adult pigs but only to a very limited extent (5 times in total, by two pigs), and was therefore not statistically analysed.

Table 3. Spearman correlation between selected social behaviours, with the p-value between brackets.

Behaviour	Nosing head	Allogrooming	Nudging	Mounting
Nosing body	0.67 (0.03)	0.68 (0.03)	0.83 (0.003)	0.89 (<0.001)
Nosing head		0.70 (0.02)	0.45 (0.19)	0.63 (0.05)
Allogrooming			0.69 (0.03)	0.52 (0.13)
Nudging				0.71 (0.02)

6.3 Social preferences (Publication 2)

The Monte Carlo test revealed the presence of preferential associations in each season, as the associations were not random. Out of the total number of connections that pigs formed, on average across the four seasons, 5.8 % consisted of strong associations, 35.7 % of weak associations and 58.5 % of no preferential associations. Autumn and winter had the highest percentage of strong associations (Table 4). The repetition of preferential associations across the seasons was analysed with the Quadratic Assignment Procedure. This highlighted only a modest positive correlation between autumn and winter and no correlation between spring, summer and any of the other seasons (Table 5). No strong associations and only two weak associations were repeated across all four seasons. However, when analysing autumn-winter, winter-spring and spring-summer separately, two strong and three weak associations remained stable between autumn and winter, only four weak associations repeated between winter and spring and seven weak associations repeated between spring and summer.

Table 4. Percentages of strong, weak or no associations for the group of 10 sows in each season.

	Autumn	Winter	Spring	Summer
Strong associations	8.9%	8.9%	2.8%	2.8%
Weak associations	31.1%	31.1%	41.7%	38.9%

No associations	60%	60%	55.6%	58.3%

Table 5. Pearson correlation coefficients between half-weight association index (HWI) matrices in the four seasons, * p<0.05.

	Autumn	Winter	Spring
Winter	0.41*		
Spring	-0.0004	0.14	
Summer	0.12	0.21	-0.16

6.4 Group cohesion in social networks (Publication 2)

Density and reciprocity showed that group cohesion and sociality were highly stable throughout the four seasons, with an average of 0.95 for both measures (1 is the maximum score; Table 6). Almost all possible connections occurred, meaning that almost all pigs interacted with each other and did so reciprocally, as shown in Fig. 3. Across the seasons, a similar level of connections occurred: 86 connections out of 90 possible connections occurred in autumn; 84 out of 90 in winter; 70 out of 72 in spring and 68 out of 72 in summer. In- and out-degree centralization values (Table 6) indicate that both the initiation and receipt of affiliative interactions among the ten pigs were weakly centralized. The weak centralization indicates that interactions were distributed reasonably homogeneously across the group members.

Table 6. Values of density, reciprocity, and mean values of in-degree and out-degree centralization in the group of sows in each season.

	Autumn	Winter	Spring	Summer
Density	0.96	0.93	0.97	0.94
Arc reciprocity	0.95	0.93	0.97	0.94
Out-degree centralization	0.33	0.23	0.29	0.24
In-degree centralization	0.17	0.23	0.16	0.21

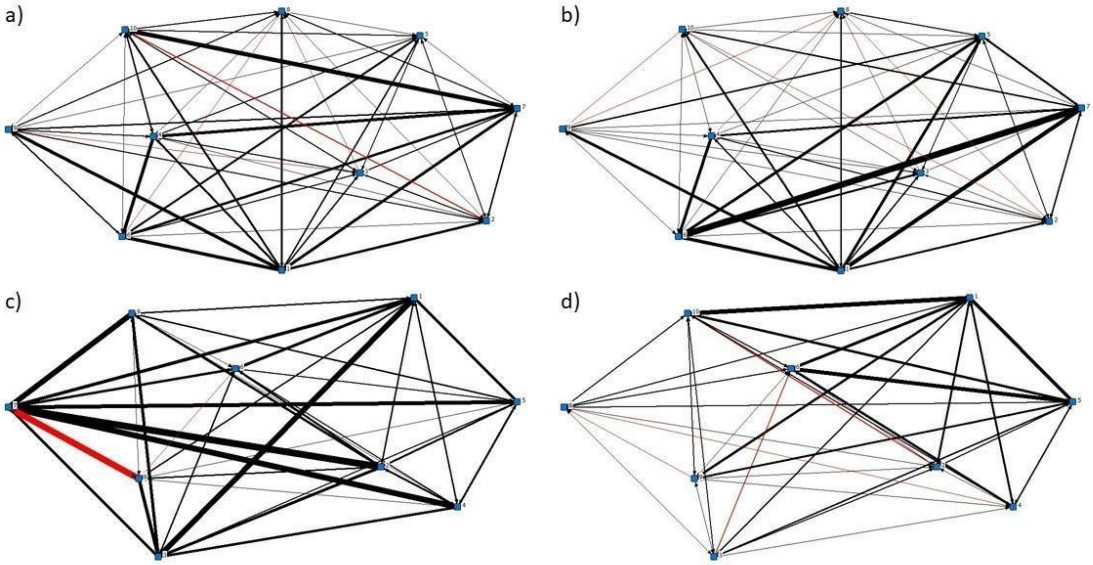

Figure 3. Graphical representation of the social network of ten sows for autumn (a), winter (b), spring (c), and summer (d). Blue squares represent nodes, which correspond to the pigs, while the lines connecting the nodes represent interactions between them. The thicker the lines, the higher the frequency of contacts between the respective nodes. Black lines represent reciprocal contact, while red lines indicate unidirectional contact.

6.5 The role of sex, dominance rank and kinship on social behaviours (Publication 3)

The PCA on the social behaviours of 96 focal pigs identified nine components with distinct loading profiles. However, only three principal components (PC1, PC2, and PC3) had eigenvalues greater than 1 and were therefore selected for further analysis. These three components combined explained a total of 60.9% of the variance among the behavioural variables (Table 7). PC1 presented strong positive loadings (≥0.5) on the frequency of making snout contact with the snout or the head of another pig, as well as on lying in body contact with a conspecific (head-to-head or in any other orientation). Behaviours belonging to PC1 were the most frequent, constituting a minimum of 8.9% and a maximum of 27.1% of the total recorded frequencies. Furthermore, almost all the individuals expressed these behaviours (97% - 100%) (Table 8). PC2 showed high positive loadings on proximity behaviours (snout-to-snout and snout-to-head). These behaviours accounted for 8.5% and 3.6% of all behavioural occurrences and were expressed by 96.9% and 85.4% of individuals

(Table 8). Consequently, they were less common than the behaviours that loaded most strongly onto PC1. PC3 exhibited high positive loadings on allogrooming and social play. PC3 behaviours occurred much less frequently (allogrooming: 0.6% and social play: 0.7%) and were expressed by only 29.2% and 33.3% of individuals (Table 8). Based on these behavioural associations, the components were labelled as follows: PC1 - *social contact*, PC2 - *proximity*, and PC3 - *social engagement*.

Sex, dominance rank and kinship did not significantly influence PC1 'social contact' or PC3 'social engagement' (Fig. 4). However, sex influenced PC2 'proximity' (estimate: 1.17 ± 0.16 SE, $p < 0.001$), indicating that males engaged more frequently in the proximity behaviours with higher loadings on this component than females (Fig. 5). Kinship had a limited effect on PC2 scores (estimate: -0.36 ± 0.18 SE, $p = 0.044$), indicating that higher relatedness was associated with lower PC2 values.

Table 7. Principal component analysis (PCA) loading scores of behaviour measurements on principal component 1 (PC1), principal component 2 (PC2) and principal component 3 (PC3). Based on social interactions observed in 96 pigs (16 groups) of 10–11 weeks of age.

Behaviour	PC1	PC2	PC3
Snout-snout contact	0.782	-0.018	0.168
Snout-snout proximity	0.059	0.851	0.080
Snout-head contact	0.815	0.104	0.096
Snout-head proximity	0.135	0.808	-0.061
Snout-body contact	0.566	0.188	0.068
Allogrooming	0.023	0.095	0.904
Lying in body contact head-to-head	0.688	-0.038	0.096
Lying in body contact any other orientation	0.742	-0.021	-0.152
Social play	0.228	-0.441	0.503
Variance explained	31%	18.2%	11.7%
Eigenvalue	2.791	1.636	1.053

781 **Table 8.** Frequency distribution of observed social behaviours. Columns show total occurrences
782 across all animals, average frequency per pig, percentage of pigs expressing the behaviour, and
783 percentage of each behaviour expression relative to total. A total of 7097 interactions were scored
784 during 160 hours of observations from 96 pigs (16 groups) aged 10–11 weeks.

Behaviour	Total occurrences	Average frequency per pig	% of pigs performing behaviour	% of total interactions
Snout-body contact	1 925	20.1	100%	27.1%
Snout-snout contact	1 628	17.0	100%	22.9%
Snout-head contact	1 186	12.4	100%	16.7%
Lying in body contact any other orientation	775	8.1	99.0%	10.9%
Lying in body contact head-to-head	634	6.6	97.9%	8.9%
Snout-snout proximity	602	6.3	96.9%	8.5%
Snout-head proximity	253	2.6	85.4%	3.6%
Allogrooming	44	0.5	29.2%	0.6%
Social play	50	0.5	33.3%	0.7%

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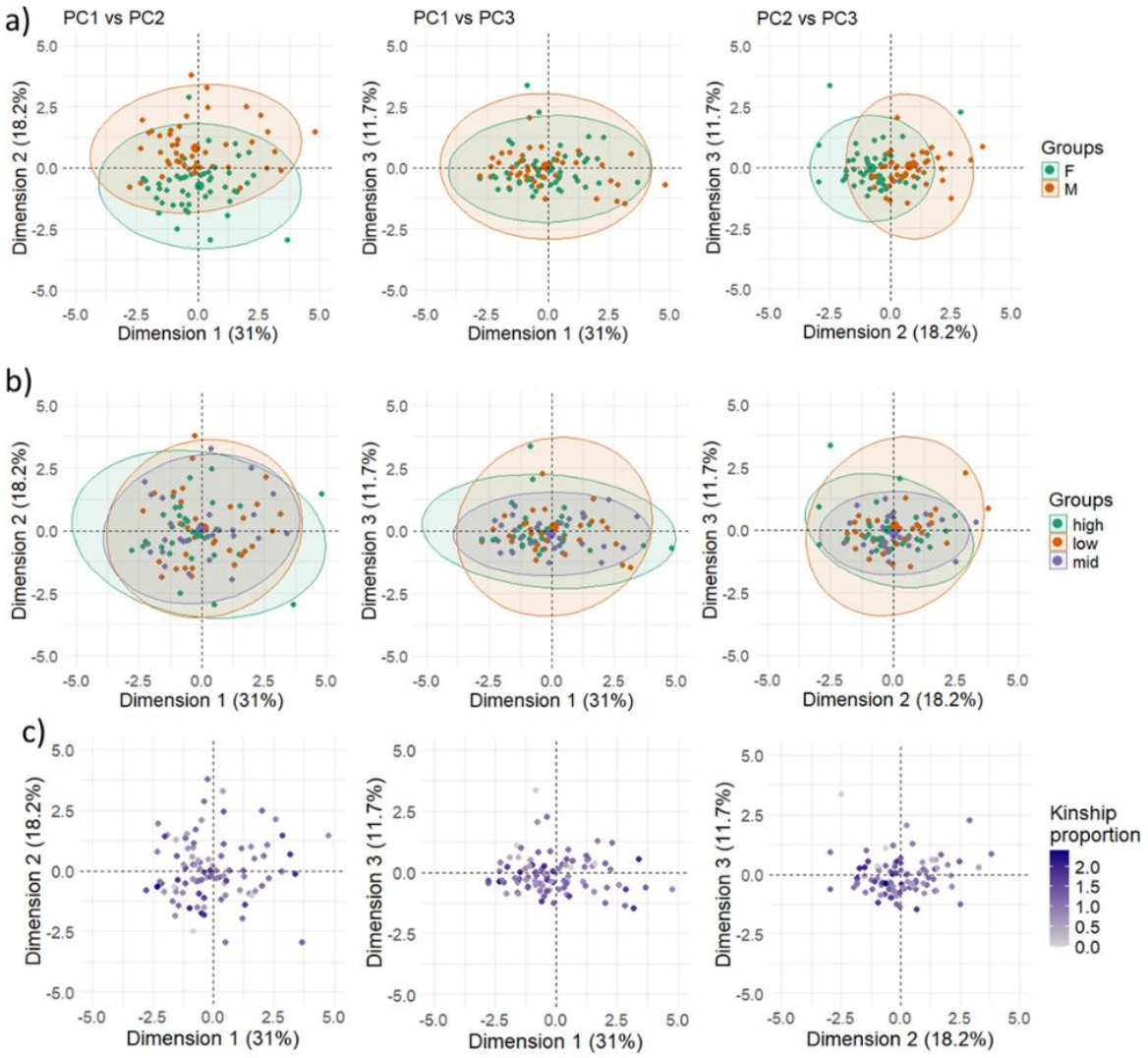

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787 **Figure 4.** Principal Component Analysis (PCA) scatterplots showing the distribution of individual
788 pigs along the first three principal components. Each plot shows a combination of the first three
789 principal components (PCs), with PCs and their variance on x- or y-axis. Each point represents one
790 individual (n = 96 pigs). a) PCA score plots grouped by sex (female, male) with 95% confidence
791 ellipses. b) PCA score plots grouped by dominance status (high, mid, low), with 95% confidence
792 ellipses. c) PCA score plots coloured by kinship proportion within the social group, where darker
793 shades indicate a higher proportion of kin interactions.

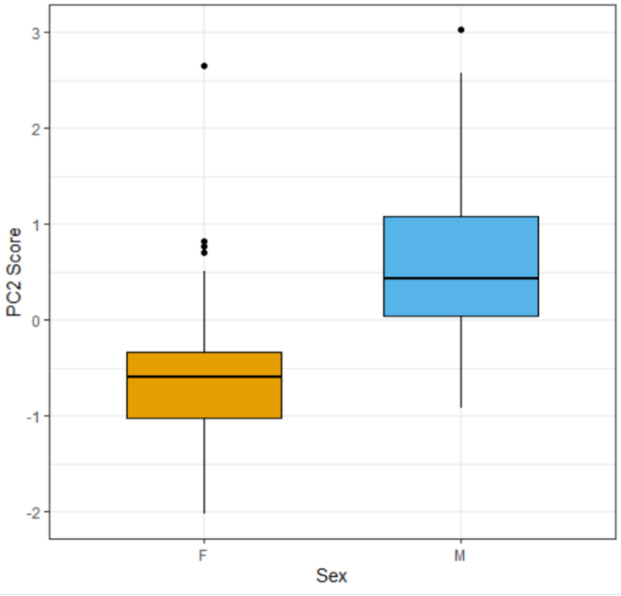

Figure 5. Principal Component Analysis (PCA) scatterplots showing the distribution of individual pigs along the first three principal components. Each plot shows a combination of the first three principal components (PCs), with PCs and their variance on x- or y-axis. Each point represents one individual (n = 96 pigs). a) PCA score plots grouped by sex (female, male) with 95% confidence ellipses. b) PCA score plots grouped by dominance status (high, mid, low), with 95% confidence ellipses. c) PCA score plots coloured by kinship proportion within the social group, where darker shades indicate a higher proportion of kin interactions.

7 General discussion

This study investigated the importance of physical contact for group-living animals, using pigs (*Sus scrofa domesticus*) as the study species. The study focused the natural expression and variation of physical contact, and the effect of environmental and individual factors. This dissertation allowed us to achieve part of the objectives of the project titled "*Adaptive significance of social touch in group-living mammals*" funded by National Science Centre (NCN), Poland, project number 2021/43/O/NZ8/00711. The study consisted of two experiments and resulted in three publications. Objective 1 was to explore the natural variation of physical contact behaviour (publication 1). In objective 2, we explored whether domestic pigs form long-term social preferences and how these relate to pigs sociability (publication 2). Finally, we investigated how, sex, age, kinship, social dominance and environmental conditions shape this variation.

Natural variation of physical contact (Publication 1)

The first objective was to study the expression of physical contact in pigs. Publication 1 highlighted that pigs spend a large part of their time in body contact, although mostly with a relatively small part of their body (extremities contact, such as the legs). As expected, they were lying least in body contact in summer, when the temperature was highest, in line with literature (Podder et al., 2022; Camerlink et al., 2022a). In summer, with an average maximum temperature of 26°C, the pigs in our study kept in contact with the extremities of their body. As they had plenty of space to lie separately, the continued physical contact suggests an affiliative need or behavioural purpose (e.g. group vigilance) to maintain these subtle contacts regardless of external conditions. However, it is also possible that this reflects an effect of winter thermoregulatory behaviour, whereby pigs habitually persist with this behaviour in summer, despite the absence of thermoregulatory purposes. Autumn was the season with the most contact behaviour, regardless of the ambient temperature. In autumn the enclosure did not yet have a hut, and without the hut it may have been colder at the floor level, which could lead to pigs keeping in closer body contact. Pigs were lying mostly head-to-head or nonparallel to each other. Considering the role of social nosing of the head in affiliative behaviour, resting in a head-to-head configuration contributes to their affiliative relationships better than other orientations (Goumon et al., 2025). Lying head-to-tail occurred clearly least, which has also been observed previously in younger pigs (Camerlink et al., 2022a). The body orientation towards others was similar between day and night, but during the day pigs were more active as compared to the night and changed position and orientation more frequently. The longer duration and greater frequency of lying head-to-tail in non-pregnant females was unexpected, and might relate to a greater interest in ano-genital nosing to assess each other's reproductive status (Pedersen, 2007).

Publication 1 also highlighted that the frequency of social nosing occurred equally across the seasons, as we expected based on the non-seasonality of general communicative and affiliative behaviours. Social nosing in pigs has various putative functions such as recognition, communication and affiliation (Camerlink and Turner, 2013). However, in this study, social nosing was considered mostly as affiliative and communicative behaviour as the group was stable and therefore would not need to nose frequently for recognition (O'Malley et al., 2022). Nosing head and nosing body moderately correlated with each other but differed in how they related to other behaviours. Nosing body correlated strongly with nudging and mounting, which are behaviours related to reproduction (Pedersen, 2007; Hemsworth and

Tilbrook, 2007) and coincide with increased social interest. Indeed, nudging and mounting (summed) occurred more frequently in the non-pregnant females, which likely were in heat. The difference in the frequency of nosing behaviours between day and night is a logical consequence of the inactivity during the night time. Overall, the results indicate that nosing the body appears to be a more general social behaviour whereas nosing the head is more specific to affiliative behaviour.

Social networks and social preferences (Publication 2)

Based on the communicative and affiliative meaning attributed to nosing behaviours and allogrooming in publication 1, these behaviours were used to study the formation of social preferences and the characteristics of social networks in pigs (publication 2). Pigs formed social preferences in each season, although around 6% of all interactions were considered to be strong preferences, one third was considered as weak preferences and approximately two thirds of all interactions were random. This is similar to other studies on social preferences in pigs (Goumon et al., 2020; Clouard et al., 2024), demonstrating that pigs in farm settings are capable of forming preferential associations. Our results are also similar to what occurs in nature, where wild boars formed non-random associations, thus likely preferential, in 20-34 % of cases (Podgórski et al., 2014). The year-long observations revealed that these social preferences are not enduring over time, as indicated by a moderate correlation between the four seasons, suggesting the absence of enduring social bonds. This alteration is likely attributable to the disruption to group cohesion caused by the removal of certain individuals for farrowing. The separation of pregnant sows prior to parturition is a standard practice in commercial farming. This is also what occurs in nature, although the separation in nature (1-2 weeks) is much shorter than occurs on a farm. Perhaps the results we have found might indicate that this natural separation may also cause some disruption to preferential relationships.

Further, we applied social network analyses, with the aim of assessing the group cohesion and stability over a relatively extended period of time. A consistently high value over time of density and reciprocity, and a weak level of group centralization, demonstrates that the group of pigs exhibited a high level of cohesion and homogeneity throughout the four seasons. As the pigs had a large space allowance, and thereby the freedom to choose whether or not to interact, their high level of cohesion appears meaningful rather than random, in line with social preferences analysis. In the natural environment, wild boars tend to cluster with related

individuals in spite of having the opportunity to disperse (Podgórski et al., 2014). We previously showed that this cohesion in domestic pigs is not necessarily related to thermal regulation (Seddaiu et al., 2024). It may be due to a need for being surrounded by familiar individuals as a result of predation risk creating benefits from being in a group and the inclusive fitness benefits of helping kin to survive rather than unrelated animals. It could also be due to a desire to maintain a threshold level of interaction, necessary to maintain familiarity (Fraser, 1974) and dominance relationships (Ewbank and Meese, 1971). To support this, contrary to what was observed in the case of social preferences, the removal and return of sows for farrowing between winter and spring, which can be seen as a potential social disruption, did not appear to significantly affect the measures of affiliation at the group level. Therefore, a reciprocity tending towards 1 across all four seasons would still demonstrate the need for a threshold level of affiliative interactions, as discussed above.

Effect of dominance rank, sex, and kinship on the expression of physical contact (Publication 3)

After exploring the natural variation in contact behaviours among pigs and then examining how pigs use these behaviours to form social preferences and stable social groups in the first experiment, experiment 2 focused on the factors underlying their expression. Specifically, it investigated which individual characteristics may influence how pigs choose interaction partners and express contact and proximity behaviours. Using a Principal Component Analysis, the data showed that dominance rank, sex, and kinship did not significantly influence PC1 scores (related to social contact), indicating that variation in social contact behaviours was not strongly related to these factors. It may indicate that physical contact is of general relevance to social life in pigs, as suggested in Seddaiu et al. (2024), and it is not strictly related to individual factors. Another principal component, PC2 (related to proximity), was characterized by high loadings of snout proximity. The finding that ‘snout contact’ (PC1) and ‘proximity’ (PC2) emerged as separate components is in line with recent literature that shows that these two similar behaviours (snout contact and snout proximity) have a subtle but distinct meanings for pigs (Khatiwada et al., 2025a; Jowett et al., 2025). Snout proximity has previously been associated with social recognition (Kristensen et al., 2001), which may switch to conflict avoidance and risk aversion during social instability (Khatiwada et al., 2025a). Males had a substantially higher score on this PC than females, showing that they are involved in more proximity-related behaviours, which relates to sex differences in pre-pubertal pigs (Camerlink et al., 2022b). Proximity-related behaviours may

facilitate conflict avoidance by allowing social assessment without direct physical contact, making information gathering more valuable and more strongly expressed in males, who face more intense competitive interactions (Camerlink et al., 2022b). In addition, pigs showed less snout proximity toward their kin, consistent with the idea that snout proximity might serve for recognition and information gathering (Kristensen et al., 2001). PC3, labelled as social engagement, was uniquely composed of allogrooming and social play. Social play in juveniles or adults and allogrooming are infrequently occurring behaviours (Newberry and Wood-Gush, 1988; Zupan et al., 2019; Seddaiu et al., 2024) with strong individual differences in their expression (play: Brown et al., 2015). We did not find an effect of individual factors on PC3. This was unexpected as previous literature indicates that play is shown more by males (Brown et al., 2015; Weller et al., 2019). The reason for this absence might be the combination of allogrooming and social play in the same component. In addition, both Brown et al. (2015) and Weller et al. (2019) studied mixed-sex groups (pre-weaning stage), whereas in the present study, pigs were housed in single-sex groups. Due to the typical group level engagement in social play (Horback, 2023), the single-sex housing can better disentangle sex differences, if present. The results suggest that pigs who initiate social play or give play invites are more socially engaged, independently of internal factors. Furthermore, while allogrooming would be assumed to occur between closely related individuals or those with a high degree of familiarity, there is so far no evidence for this (Clouard et al., 2024).

8 Conclusion

The dissertation outlined the diversity and occurrence of physical contact in pigs, as well as how internal and external factors can shape this variation and affect their social life. In conclusion, the results from the two experiments showed that:

1. Body contact varied between seasons, with less body contact in summer when the temperature was highest. However, social behaviours and body contact remained present regardless of season and temperature. This confirmed the non-seasonality and importance of general communicative and affiliative behaviours, which contribute to the expression of social preferences.
2. Pigs form social preferences, although mostly weak and did not endure over a longer period of time. Pigs can maintain a cohesive and stable social structure across four seasons, despite the removal of group members. The high density and reciprocity indicate that nosing body and nosing head are common and potentially of large importance to the social lives of pigs.
3. Individual characteristics of dominance rank, sex and the relative frequency of kinship-based interactions partially influenced the expression of individual profiles based on social behaviours. The results emphasized the relevance of distinguishing between direct physical contact and those performed in close social proximity without making contact.

9 References

Abdi, H., & Williams, L. J. (2010). Principal component analysis. *Wiley interdisciplinary reviews: computational statistics*, *2*(4), 433-459.

Andersen, I. L., Bøe, K. E., & Kristiansen, A. L. (1999). The influence of different feeding arrangements and food type on competition at feeding in pregnant sows. *Applied Animal Behavior Science*, *65*(2), 91-104.

Andersen, I. L., Roussel, S., Ropstad, E., Braastad, B. O., Steinheim, G., Janczak, A. M., Jørgensen, G.M., & Bøe, K. E. (2008). Social instability increases aggression in groups of dairy goats, but with minor consequences for the goats' growth, kid production and development. *Applied Animal Behaviour Science*, *114*(1-2), 132-148.

Arey, D. S., & Edwards, S. A. (1998). Factors influencing aggression between sows after mixing and the consequences for welfare and production. *Livestock Production Science*, *56*(1), 61-70.

Babicz, M., Hałabis, M., Skałecki, P., Domaradzki, P., Litwińczuk, A., Kropiwiec-Domańska, K., & Łukasik, M. (2020). Breeding and performance potential of Puławska pigs–a review. *Annals of Animal Science*, *20*(2), 343-354.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of statistical software*, *67*, 1-48.

Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). Ucinet for Windows: Software for social network analysis. *Harvard, MA: analytic technologies*, *6*, 12-15.

Brown, S. M., Klaffenböck, M., Nevison, I. M., & Lawrence, A. B. (2015). Evidence for litter differences in play behaviour in pre-weaned pigs. *Applied Animal Behaviour Science*, *172*, 17-25.

Büttner, K., Czycholl, I., Mees, K., & Krieter, J. (2020). Social network analysis in pigs: Impacts of significant dyads on general network and centrality parameters. *Animal*, *14*(2), 368-378.

Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behavior*, *35*(5), 1454-1469.

Camerlink, I., Bijma, P., Kemp, B., & Bolhuis, J. E. (2012). Relationship between growth rate and oral manipulation, social nosing, and aggression in finishing pigs. *Applied Animal Behaviour Science*, *142*(1-2), 11-17.

Camerlink, I., & Turner, S. P. (2013). The pig's nose and its role in dominance relationships and harmful behaviour. *Applied Animal Behaviour Science*, *145*(3-4), 84-91.

Camerlink, I., Arnott, G., Farish, M., & Turner, S. P. (2016). Complex contests and the influence of aggressiveness in pigs. *Animal Behaviour*, *121*, 71-78.

Camerlink, I., Scheck, K., Cadman, T., & Rault, J. L. (2022a). Lying in spatial proximity and active social behaviors capture different information when analyzed at group level in indoor-housed pigs. *Applied Animal Behavior Science*, *246*, 105540.

Camerlink, I., Farish, M., Arnott, G., & Turner, S. P. (2022b). Sexual dimorphism in ritualized agonistic behaviour, fighting ability and contest costs of Sus scrofa. *Frontiers in zoology*, *19*(1), 13.

Cascio, C. J., Moore, D., & McGlone, F. (2019). Social touch and human development. *Developmental cognitive neuroscience*, 35, 5-11.

Chua, B., Coenen, E., Van Delen, J., & Weary, D. M. (2002). Effects of pair versus individual housing on the behavior and performance of dairy calves. *Journal of dairy science*, *85*(2), 360-364.

Clouard, C., Resmond, R., Prunier, A., Tallet, C., & Merlot, E. (2022). Exploration of early social behaviors and social styles in relation to individual characteristics in suckling piglets. *Scientific reports*, *12*(1), 2318.

Clouard, C., Foreau, A., Goumon, S., Tallet, C., Merlot, E., & Resmond, R. (2024). Evidence of stable preferential affiliate relationships in the domestic pig. *Animal Behavior*, *213*, 95-105.

Durrell, J. L., Sneddon, I. A., O'connell, N. E., & Whitehead, H. (2004). Do pigs form preferential associations? *Applied Animal Behavior Science*, *89*(1-2), 41-52.

Ekkel, E. D., Spoolder, H. A., Hulsegge, I., & Hopster, H. (2003). Lying characteristics as determinants for space requirements in pigs. *Applied Animal Behavior Science* , *80*(1), 19-30.

Ewbank, R., & Meese, G. B. (1971). Aggressive behaviour in groups of domesticated pigs on removal and return of individuals. *Animal Science*, *13*(4), 685-693.

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of animal ecology*, *84*(5), 1144-1163.

Farroni, T., Della Longa, L., & Valori, I. (2022). The self-regulatory affective touch: a speculative framework for the development of executive functioning. *Current Opinion in Behavioral Sciences*, 43, 167-173.

Fraser, D. (1974). The behavior of growing pigs during experimental social encounters. *The Journal of Agricultural Science*, *82*(1), 147-163.

Gero, S., Bejder, L., Whitehead, H., Mann, J., & Connor, R. C. (2005). Behaviorally specific preferred associations in bottlenose dolphins, Tursiops spp. *Canadian Journal of Zoology*, *83*(12), 1566-1573.

Ginsberg, J. R., & Young, T. P. (1992). Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, *44*(1), 377-379.

Glickman, M. E. (1999). Parameter estimation in large dynamic paired comparison experiments. *Journal of the Royal Statistical Society Series C: Applied Statistics*, *48*(3), 377-394.

Goumon, S., Illmann, G., Leszkowová, I., Dostalová, A., & Cantor, M. (2020). Dyadic affiliate preferences in a stable group of domestic pigs. *Applied Animal Behavior Science*, *230*, 105045.

Goumon, S., Jowett, S., Khatiwada, S., & Camerlink, I. (2025). Peer social bonds in farm animals. A*nimal*, 101687.

Grandi, L. C., & Bruni, S. (2024). COVID-19 and human touch, two sides of the same coin: an opinion article about touch deprivation and future directions. *BioMed*, *4*(4), 366-371.

Hanneman, R. A., & Riddle, M. (2005, January). *Introduction to social network methods*.

Hemsworth, P. H., & Tilbrook, A. J. (2007). Sexual behavior of male pigs. *Hormones and Behavior*, *52*(1), 39-44.

Herpin, P., Damon, M., & Le Dividich, J. (2002). Development of thermoregulation and neonatal survival in pigs. *Livestock production science*, *78*(1), 25-45.

Herskin, M. S., & Jensen, K. H. (2000). Effects of different degrees of social isolation on the behaviour of weaned piglets kept for experimental purposes. *Animal Welfare*, *9*(3), 237-249.

Horback, K. (2023). Nosing around: Play in pigs. *Animal Behavior and Cognition*, *2*(2), 186.

Huynh, T.T.T., Aarnink, A.J.A., Gerrits, W.J.J., Heetkamp, M.J.H., Canh, T.T., Spoolder, H.A.M., Kemp, B., & Verstegen, M.W.A. (2005). Thermal behavior of growing pigs in response to high temperature and humidity. *Applied Animal Behavior Science*, *91*(1-2), 1-16.

Jablonski, N. G. (2021). Social and affective touch in primates and its role in the evolution of social cohesion. *Neuroscience*, 464, 117-125.

Jarvis, S., D'Eath, R. B., Robson, S. K., & Lawrence, A. B. (2006). The effect of confinement during lactation on the hypothalamic–pituitary–adrenal axis and behaviour of primiparous sows. *Physiology & behavior*, *87*(2), 345-352.

Jensen, P. (1980). An ethogram of social interaction patterns in group-housed dry sows. *Applied Animal Ethology*, *6*(4), 341-350.

Jørgensen, G. H. M., Andersen, I. L., & Bøe, K. E. (2009). The effect of different pen partition configurations on the behaviour of sheep. *Applied Animal Behaviour Science*, *119*(1-2), 66-70.

Jowett, S. L., Silk, M. J., Lee, V., Turner, S. P., & Camerlink, I. (2025). Characterizing nose behaviors in pigs after mixing using social network analysis. *Animal*, *19*(8), 101585.

Kaiser, H. F. (1960). The application of electronic computers to factor analysis. *Educational and psychological measurement*, *20*(1), 141-151.

Kassambara, A., & Mundt, F. (2016). Factoextra: extract and visualize the results of multivariate data analyses. *CRAN: Contributed Packages* .

Khatiwada, S., Lee, V. E., Turner, S. P., & Camerlink, I. (2025a). Trade-offs between proximity and physical contact during group integration in pigs (Sus scrofa domesticus). *Current Zoology*, zoaf056.

Khatiwada, S., Lee, V., Turner, S. P., & Camerlink, I. (2025b). Temporal social network structures based on snout contact during group integration in pigs. *Applied Animal Behavior Science*, 106838.

Kristensen, H. H., Jones, R. B., Schofield, C. P., White, R. P., & Wathes, C. M. (2001). The use of olfactory and other cues for social recognition by juvenile pigs. *Applied Animal Behavior Science*, *72*(4), 321-333.

Li, Y., Zhang, H., Johnston, L. J., & Martin, W. (2018). Understanding tail-biting in pigs through social network analysis. *Animals*, *8*(1), 13.

McCort, W. D., & Graves, H. B. (1982). Social dominance relationships and spacing behavior of swine. *Behavioral Processes*, *7*(2), 169-178.

Meynhardt, H., 1982. Schwarzwildreport. Mein Leben Unter Wildschweinen. Neumann-Neudamm, Germany, Melsungen.

Meurens, F., Summerfield, A., Nauwynck, H., Saif, L. & Gerdts, V. (2012). The pig: a model for human infectious diseases. *Trends in microbiology,* 20(1), 50-57.

Miller, K., & Wood-Gush, D. G. M. (1991). Some effects of housing on the social behavior of dairy cows. *Animal Science*, *53*(3), 271-278.

Newberry, R. C., Wood-Gush, D. G. M., & Hall, J. W. (1988). Playful behavior of piglets. *Behavioral Processes*, *17*(3), 205-216.

Newberry, R., & Swanson, J. (2001). Breaking social bonds. In *Social behaviour in farm animals* (pp. 307-331). Wallingford UK: CABI Publishing.

O'Malley, C. I., Steibel, J. P., Bates, R. O., Ernst, C. W., & Siegford, J. M. (2022). The Social Life of Pigs: Changes in affiliative and agonistic behaviors following mixing. *Animals*, *12*(2), 206.

Packheiser, J., Hartmann, H., Fredriksen, K., Gazzola, V., Keysers, C., & Michon, F. (2024). A systematic review and multivariate meta-analysis of the physical and mental health benefits of touch interventions. *Nature human behaviour*, *8*(6), 1088-1107.

Pedersen, L. J. (2007). Sexual behaviour in female pigs. *Hormones and behavior*, *52*(1), 64-69.

Petersen, V., Recén, B., & Vestergaard, K. (1990). Behaviour of sows and piglets during farrowing under free-range conditions. *Applied Animal Behaviour Science*, *26*(1-2), 169-179.

Petherick, J. C., & Blackshaw, J. K. (1987). A review of the factors influencing the aggressive and agonistic behaviour of the domestic pig. *Australian Journal of Experimental Agriculture*, *27*(5), 605-611.

Podder, M., Bera, S., Naskar, S., Sahu, D., Mukherjee, J., & Patra, A. K. (2022). Physiological, blood-biochemical and behavioral changes of Ghoongroo pigs in seasonal heat stress of a hot-humid tropical environment. *International journal of biometeorology*, *66*(7), 1349-1364.

Podgórski, T., Lusseau, D., Scandura, M., Sönnichsen, L., & Jędrzejewska, B. (2014). Long-lasting, kin-directed female interactions in a spatially structured wild boar social network. *PLoS One* , *9*(6), e99875.

Ruis, M. A., te Brake, J. H., Engel, B., Buist, W. G., Blokhuis, H. J., & Koolhaas, J. M. (2001). Adaptation to social isolation: acute and long-term stress responses of growing gilts with different coping characteristics. *Physiology & behaviour*, *73*(4), 541-551.

Seddaiu, P., Turner, S. P., & Camerlink, I. (2024). Cross-seasonal and diurnal variation in physical contact between sub-adult pigs. *Applied Animal Behaviour Science*, *278*, 106379.

Stanged, G., & Jensen, P. (1991). Behaviour of semi-naturally kept sows and piglets (except suckling) during 10 days postpartum. *Applied Animal Behaviour Science*, *31*(3-4), 211-227.

Steinerová, K., Parker, S. E., Brown, J. A., & Seddon, Y. M. (2024). The promotion of play behaviour in grow-finish pigs: the relationship between behaviours indicating positive experience and physiological measures. *Applied Animal Behaviour Science*, *275*, 106263.

Stephenson, A., & Sonas, J. (2020). *PlayerRatings: Dynamic updating methods for player ratings estimation. R package version 1.1-0*.

Swindle, M. M., Makin, A., Herron, A. J., Clubb, F. J. Jr & Frazier, K. S. (2012). Swine as models in biomedical research and toxicology testing. *Veterinary pathology*, *49*(2), 344-356.

Tabachnick, B. G., Fidell, L. S., & Ullman, J. B. (2007). *Using multivariate statistics* (Vol. 5, pp. 481-498). Boston, MA: pearson.

Team, R. C. (2020). RA language and environment for statistical computing, R Foundation for Statistical. *Computing*.

Thomas, P. A., & Kim, S. (2021). Lost touch? Implications of physical touch for physical health. *The Journals of Gerontology: Series B*, 76(3), e111-e115.

Vieira, A. D. P., Von Keyserlingk, M. A. G., & Weary, D. M. (2010). Effects of pair versus single housing on performance and behavior of dairy calves before and after weaning from milk. *Journal of dairy science*, *93*(7), 3079-3085.

Von Mohr, M., Kirsch, L. P., & Fotopoulou, A. (2021). Social touch deprivation during COVID-19: effects on psychological well-being and craving for interpersonal touch. *Royal Society open science*, *8*(9).

Walker, S. C., Trotter, P. D., Swaney, W. T., Marshall, A., & Mcglone, F. P. (2017). C-tactile afferents: Cutaneous mediators of oxytocin release during affiliative tactile interactions?. *Neuropeptides*, *64*, 27-38.

Weller, J. E., Camerlink, I., Turner, S. P., Farish, M., & Arnott, G. (2019). Playful pigs: early life play-fighting experience influences later life contest dynamics. *Animal Behaviour*, *158*, 269-279.

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal behaviour*, *75*(2), 333-344.

Whitehead, H., & James, R. (2015). Generalized affiliation indices extract affiliations from social network data. *Methods in Ecology and Evolution*, *6*(7), 836-844.

Wickham, H. (2016). Elegant graphics for data analysis.

Yin, G., Liu, H., Li, X., Quan, D., & Bao, J. (2016). Effect of Farrowing Environment on Behavior and Physiology of Primiparous Sows with 35-day Lactation. *International Journal of Applied Research in Veterinary Medicine*, *14*(2).

Zupan, M., Rehn, T., de Oliveira, D., Malovrh, Š., & Keeling, L. (2019). Individual play patterns stimulated by a familiar object are group-driven. *Scientific Reports*, *9*(1), 6092.

10 Appendices

10.1 Author's contribution to each publication

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

Seddaiu, P., Turner, S.P., Camerlink, I. (2024). Cross-seasonal and diurnal variation in physical contact between sub-adult pigs. *Applied Animal Behavior Science.*

Lp.	**Imię i nazwisko** ***(name and surname)***	**Opis udziału autora** ***(Description of the author's participation)***	**Jednostka** ***(Institution)***
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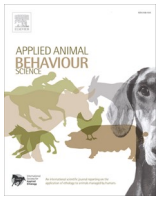

Cross-seasonal and diurnal variation in physical contact between sub-adult pigs

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ABSTRACT

Social touch is an important aspect of social relationships and has a major influence on development and health. However, in many species the occurrence and function of social touch is unknown. Pigs have frequent physical contact but this behaviour is largely unexplored. The aim of this study was to investigate the undisturbed variation in physical contact between pigs, and to assess diurnal and seasonal influences. A stable group of ten Puławska sub-adult female pigs was observed for 406 h across four seasons during the day and night, by continuous observations on an individual level (406 h / pig). They were housed indoors (112 m^2 pen) on straw bedding. The ethogram distinguished the amount of surface contact between pigs when lying, the orientation to others, social nosing, other non-agonistic social behaviour and agonistic behaviours. Resting location within the pen was recorded 48 times per pig, and dominance relationships were calculated from agonistic interactions. Data were analysed with mixed models accounting for repeated observations. Pigs spent on average 40 % of their time lying in body contact, most often lying with their extremities in contact (71 %), followed by lying in partial body contact (16 %) or full body contact (13 %) and were frequently nosing the head and body of others. The duration of lying in any type of contact, as well as agonistic behaviour, was influenced by season, with the longest durations in autumn. In summer, the duration of partial body contact was lowest, but full body contact was unaffected by season. Nosing behaviour remained constant throughout the year. Pigs lay in contact more during the night, while showing more social behaviours during the day. Pigs mostly lay in nonparallel orientation or head-to-head, but clearly least in the head-to-tail orientation. Season influenced the frequency of lying head-to-head and head-to-tail, but not lying nonparallel. The coefficient of variation of the lying location was influenced by season. Allo-grooming, mounting, and nudging were shown infrequently and mostly by specific individuals. In conclusion, when at a large space allowance, pigs spend nearly half of their time in body contact, even during the higher temperatures in summer. This shows that social touch, including affiliative behaviour, has an important role in pigs' social life, and remains largely unaffected by external influences.

1. Introduction

Physical contact, such as body contact and gentle touch, has an important role in the health and welfare of group-living species (Cascio et al., 2019; Jablonski, 2021; Thomas and Kim, 2021). Physical contact has practical biological functions such as thermoregulation (Gilbert et al., 2010), hygiene maintenance (Sánchez-Villagra et al., 1998), and protection from predators (Gilbert et al., 2010) but is also indispensable for effective communication (Kutsukake and Castles, 2001; Hertenstein et al., 2006) and maintaining group cohesion (Dunbar, 1991; Lehmann et al., 2007) within groups of social animals, and can reinforce social bonds (primates: Jablonski, 2021). In species such as non-human primates, deliberate physical contact can be expressed through allo-grooming, which contributes to coat hygiene (Sánchez-Villagra et al., 1998), the development of social bonds and the resolution of conflicts within the group (Silk et al., 2006). Given the known benefits of gentle physical contact in primates (Romero et al., 2010; Grandi and Ishida, 2015), it is surprising that in other species social touch has received relatively little research attention in comparison to potentially harmful behaviours (Mellor and Beausoleil, 2015). Where it has been studied in non-primate species, physical touch appears to be important. For example, in rodents, the amount of licking/grooming of pups (as a

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form of maternal care) influences offspring neurobiology and cognitive development (Champagne et al., 2001; Fish et al., 2004).

Under farm conditions, animals usually live in restricted housing conditions, and factors such as space availability (cattle: Miller and Wood-Gush, 1991), pen design (pigs: Andersen et al., 1999), group size (sheep: Jørgensen et al., 2009) and social instability (goats: Andersen et al., 2008) can impact the quantity and quality of their physical contact with one another. Under limited space allowance, animals may have limited choice regarding whom to be in contact with, and may be forced to be in physical contact against their will. This could potentially lead to social stress and conflict, as subordinate animals may be unable to distance themselves from dominant ones. Dominant animals have indeed been shown to be spaced further away from others (e.g., pigs: Camerlink et al., 2014), showing a potential relationship between dominance rank and contact behaviour. At the same time, social species that are kept in social isolation, such as single housed calves (Chua et al., 2002; Vieira et al., 2010) and sows in gestation crates (Jarvis et al., 2006; Yin et al., 2016), may suffer from the lack of physical contact. The effect of social isolation has been well-studied with the clear conclusion that it is highly stressful for social species (pigs: Herskin and Jensen, 2000; mice: Ieraci et al., 2016; rats: Weiss et al., 2004). However, where farm animals are managed in social groups, the importance of the quantity and quality of physical contact has received limited attention. Overall, there is a lack of information on the natural frequency and duration of contact, and what types of contact are preferred, under conditions in which animals are able to express these preferences. Therefore, for most farm livestock species, the natural variation in contact behaviour is largely unknown.

The aim of this study was to describe the natural variation of gentle physical contact in group-housed pigs (*Sus scrofa domesticus*). Pigs rest frequently in body contact (Ekkel et al., 2003; Camerlink et al., 2022), and may huddle when cold (Huynh et al., 2005). Resting in body contact, especially at a young age, helps them to remain in their thermoneutral zone (Herpin et al., 2002) while at higher temperatures they are more likely to space apart (Huynh et al., 2005). They also make frequent snout contact, which serves various purposes such as affiliation, recognition (Camerlink and Turner, 2013) and mother-offspring bonding (Petersen et al., 1990; Stanged and Jensen, 1991). Initial work on social nosing showed that pigs which received more social nosing had a higher growth rate (Camerlink et al., 2012), suggesting a beneficial effect of snout contact. Allo-grooming does occur in pigs but has rarely been studied (Goumon et al., 2020; Camerlink et al., 2022), and these studies, which were conducted mostly in juvenile pigs, showed that allo-grooming occurred infrequently. It is unknown whether the limited occurrence may be due to the housing conditions or the age at which pigs were studied.

Based on the existing literature, we predict that the frequency of body contact will vary depending on pigs' thermoregulatory needs, with more body contact in colder seasons and less body contact in summer. However, we expect the frequency of affiliative contact such as snout contact and allo-grooming to remain stable throughout the year due to its importance in communication and social cohesion.

2. Methods

The study was observational and therefore did not require ethics approval according to the national guidelines (non-invasive studies are not considered by the local ethical committee). For individual recognition, animals were marked with a marker crayon, which they readily accepted without moving away and therefore this did not form a stressor. Pigs were inspected daily for their health and received adequate veterinary care when needed.

2.1. Animals and housing

A herd of ten sub-adult females of the native Polish Puławska breed were studied at the pig research farm of the Institute of Genetics and Animal Biotechnology of the Polish Academy of Science, Warsaw, Poland. The group consisted of seven full-sibs from one litter, two full sibs from another litter and one half-sib. They originated from the same breeder, where the gilts were in the same group from weaning to 50 kg and thereafter split into smaller groups. From arrival at the research facilities (3 months prior to the study) they were kept as one group, under the same conditions and management as during the study. At the onset of the study, pigs were eight months old and had an average weight of 106 kg (range 80 – 128 kg), whereas they were 15 months old and approximately double the weight at the end of observations. Since their arrival at the facility, pigs were housed in a barn with natural ventilation and no source of heating. The Puławska breed is well adapted to the colder climate and therefore is well-suited to be kept at lower temperatures than in commercial farms. The group was kept in an indoor pen of 16 m × 7 m (movement area of 108 m^2), which guaranteed an area of 10.8 m^2 per pig, whereas the minimum required by EU Council Directive 2008/120/EC is at least 1.64 m^2 per gilt and 2.25 m^2 per sow. The pen had a concrete floor with straw bedding (ca. one 500 kg straw bale). The bedding was changed once a week during autumn, winter and spring, and twice a week during summer, in order to always keep at least ca. 500 kg of bedding straw on the floor. Additionally, the pigs were provided with ca. 10 kg of fresh straw ca. 30 min. before the start of the observations, in order to keep the bedding area clean. From winter onwards, a covered hut (dimensions: 6.0 × 2.0 × 1.5 m; 1.2 m^2 / pig) made from wood was provided within the barn for the pigs to stay warm. Pigs were floor fed twice daily (at 9 am and 3 pm) by spreading the food in a line across the floor. Feed was a commercial fine-ground sow meal (10.26 MJ/kg;16 kg feed when dry for the whole group) which was mixed with water and ca. 150 ml rapeseed oil. The same feed type and quantity was provided throughout the year. Water was available *ad libitum* from two drinkers. The building had natural daylight and artificial lights were on from 07:00–18:00 h, which together provided an illumination of 77–80 lux during daylight hours. The ambient temperature was recorded with two thermometers (Xiaomi Mi temperature and humidity monitor 2) for the daily average, and by a data logger (Eliotech RC-5). One thermometer and the data logger were placed just outside the pen enclosure, while the second thermometer was placed inside the hut.

2.2. Behavioural observations

Behavioural observations were conducted across four seasons within one twelve-month period (autumn and winter 2022, spring and summer 2023). Behaviour was observed day and night. Across the year, four to five females per season were pregnant (four in autumn and winter, and five in spring and summer), which was accounted for in the statistical analysis. Due to their pregnancies, six out of ten gilts were temporarily relocated (outside the group) for farrowing in between two observation blocks and returned to the group at least one week before the next observation block. As the group was stable since a young age, and pigs were mostly sisters, the disruption of reintroducing pigs subsided within the course of a few days. The autumn, winter and spring observations included 10 pigs, while the summer observations included nine pigs. Studying a small group of animals allowed us to obtain more detailed and longitudinal data that would not have been possible with a large number of animals, and thus better suited our current aim to investigate cross-seasonal and diurnal patterns in natural contact behaviour in detail.

One person conducted continuous behavioural observations, using the ethogram in Table 1 while noting the actor and recipient of each behaviour. Only active lying down was scored (Goumon et al., 2020), which means that contact behaviour was only scored for the actor, i.e., the animal that was actively making the movement of lying down beside another pig, whereas the recipient who was already lying was not additionally recorded as lying in contact.

Behavioural observations were conducted using the Animal

Table 1
Ethogram of behaviours scored live and from video. Aggression and agonistic behaviour were scored during observation hours, and additionally at 15.00 during feeding for the calculation of dominance relationships.

Behaviour	Description
Social behaviour (frequency)	
Aggression	Bites while the snout contacts the skin of another pig, resulting in potential skin damage; includes reciprocal fights.
Agonistic behaviour	Displacing another individual from a resource (with or without physical contact), head knocks, directing an open-mouth bite to the other without making physical contact, chasing the other without bites that make physical contact.
Allo-grooming	Gently nibbles or licks the body or head of another pig; does not cause acute skin damage to the other pig.
Belly nosing	Repetitive and slightly forceful up and down snout movement on the belly of another pig.
Mounting	Places both forelegs on the body of another standing or lying pig.
Nosing body	Touches the body of another pig with its nose disc, excluding the head.
Nosing head	Touches another pig's head with its nose disc; can include the snout; excludes allo-grooming.
Nudging	Gives a short non-forceful push to another pig (any part of body) with its snout.
Resting behaviour (frequency and duration)	
Full body contact* (Fig. 1)	Lying with a minimum of approximately 75 % of its body against its neighbour.
Partial body contact* (Fig. 1)	Lying with approximately 25 – 74 % of its body against its neighbour.
Extremities contact* (Fig. 1)	Lying with approximately 1 – 24 % of its body against its neighbour; includes contact of only the snout, legs, tail or other small portion of the body.

* For these behaviours the orientation (parallel head-to-head, parallel head-to-tail, or nonparallel, depicted in Fig. 1) was scored as a modifier.

Behaviour Pro App, version 1.2 (University of Kent, Canterbury, UK), installed on an iPad. Pigs were marked for individual identification with animal marking crayon (Raidex crayon, red or yellow) on their back every day, and marking was completed at least 30 min before the start of the observations. Additionally, pigs were recognized by their individual coat patterns. Daytime observations took place between 09.30 and 18:00 h and were scheduled into blocks of 2 or 2.5 h, with a maximum of 5 hours (2 observation blocks) a day. The timing of the observation blocks was balanced across the observation days. Daytime observations were conducted live, except for some days during the winter season. The observer positioned himself stationary outside the pen, largely out of sight of the pigs, and did not interact with them. Night time observations were recorded on sports cameras (AKASO EK7000), one in the main area and one inside the hut, and lasted from 18:30–06:30 h (12 h). Night time observations were obtained from five night recordings balanced across the observation weeks. Four orange LED light tubes (126 cm length) were used to guarantee visibility, providing an illumination of 25–30 lux, but were sufficiently dim to prevent disturbance to the pigs during night observations. In each season, 101.5 hours of observations (41.5 h daytime and 60 h nighttime) were carried out across ten days within a two-week time frame. All behaviours were scored as frequencies while for lying in body contact and other body contact (see ethogram) the duration was also recorded.

2.3. Dominance hierarchy

To assess dominance relationships, additional observations for agonistic behaviour and for aggression were carried out during feeding, using the ethogram in Table 1. Behavioural observations were performed live by a single observer, using the Animal Behaviour Pro App version 1.2 (University of Kent, Canterbury, UK). Observations were conducted for 30 min a day starting immediately after providing food at 15:00 h, with five observation blocks per season. From the sum of agonistic and aggressive behaviour the Modified David's Score (MDS) was calculated, using Socprog (2.9 version).

2.4. Lying location

The lying location was recorded in order to assess whether pigs preferred certain locations in the barn, which could reflect preferences for location rather than social partner (Jowett et al., 2023). The group pen was divided into 2 × 2 m Section (4 m^2), marked by small white tapes on the pen wall. The last row of sections was 1.7 × 2.0 m. Over the width of the pen there were four sections and over the length there were eight sections, resulting in 32 sections in total. The lying location was scored when the pig was lying down with more than 50 % of its body in a section. If a pig was lying down with 50 % of its body in one section and 50 % in the adjacent one, the section where the pig's head was located was scored. The lying location of each pig was scored every 30 min (regardless of whether pigs changed location in between) starting at 09:30 h, eight times a day across six days per season.

2.5. Data analysis

Data were analysed in SAS version 9.4 (SAS Institute Inc., Cary, NC, USA), using three datasets.

Dataset 1 contained the behavioural data per sow, averaged by season (no repeated observations), which was used to investigate correlations between specific behaviours. Due to the variables not being normally distributed, Spearman correlations were used.

In dataset 2, behavioural data were summed per animal by time of day (day or night) and season (4 seasons), resulting in eight data lines (i.e., repeated observations) per individual. The durations and the frequencies were converted to 12-hour averages, so that the behaviours during the day and night were both expressed as average per 12 hour time block. Durations (initially in seconds) were converted to minutes. Behaviours were analysed using mixed models (MIXED Procedure) with a Gaussian distribution. The response variable was the behaviour, and the predictor variables were season (4 seasons), daytime (day / night), their interaction (season*daytime), the MDS (covariate) and whether the females were pregnant or not. When pregnancy did not significantly influence the response variable it was removed from the model. The animal ID was entered as a random statement to account for repeated observations per animal (10 subjects, 8 observations per subject). As the model was used multiple times (for each behaviour), we corrected for multiple testing using the Bonferroni adjustment. Behaviours for which the model residuals did not follow a normal distribution (also not after transformation) due to infrequent occurrence were reported descriptively.

Dataset 3 included the lying locations across the 32 sections (data per animal, with the frequency of lying down per section). The percentage of location use (out of total frequency of location use of all pigs) was used to make heat maps. From the 32 sections the coefficient of variation (CV) was calculated to assess pigs' variation in resting location (i.e., section use). The relationship between the CV of location use and season was analysed in a mixed model (MIXED procedure), with CV as response variable and season as predictor variable. Animal ID was entered as a random variable to account for repeated observations.

Values are means with standard errors (SE) unless indicated otherwise.

3. Results

Pigs spent on average 40 ± 9 % (SD) of the observed time in body contact, which was mostly lying with their extremities in contact (71 ± 4 %, SD), followed by lying in partial body contact (16 ± 5 %, SD) or full body contact (13 ± 7 %, SD) and frequently showed contact behaviours, of which the most frequent was nosing the head and body (Fig. 1).

Three types of behavioural categories could be distinguished from the data: frequently occurring behaviours which were subject to

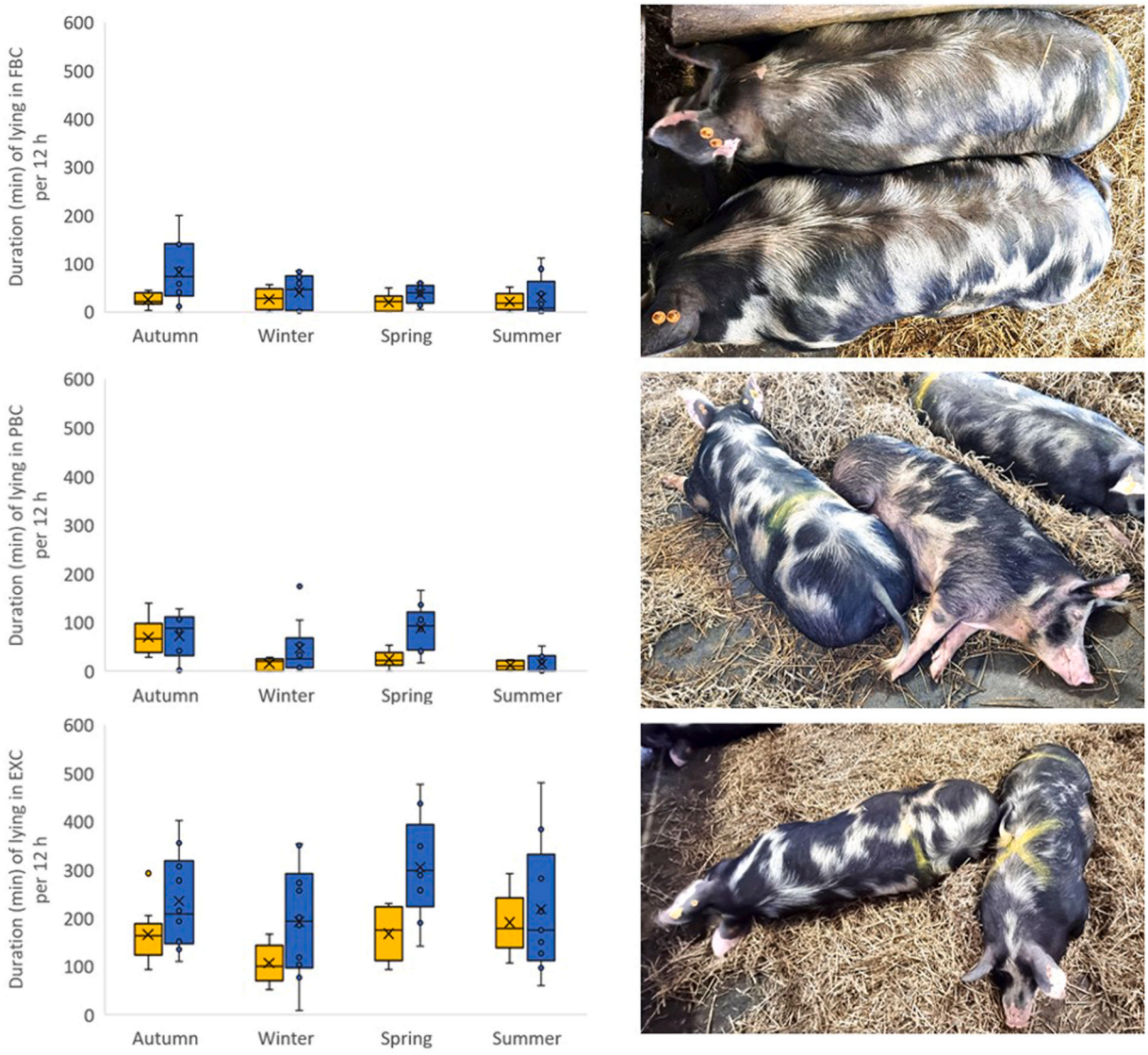

Fig. 1. Boxplots of duration in minutes per 12 h time block, by season and day (in yellow) and night (in blue), for lying in full body contact (FBC), partial body contact (PBC), and with extremities in contact (EXC). Boxes range from 1st-3rd quartile while the inner line represents the median and the X the average. Whiskers below and above the boxes show the minimum observation above the lower fence (Q1 - 1.5 IQR) and the maximum observation below the upper fence (Q3 + 1.5 IQR). Outliers are represented as solid circles. The photo to the right of each boxplot illustrates the contact behaviour, including additionally the different lying orientations (parallel head-to-head, parallel head-to-tail and nonparallel).

seasonal changes; frequently occurring behaviours which remained constant throughout the year; and infrequently occurring behaviours which were only shown by a few individuals, which are described below. Maximum and minimum air temperatures in the building and coefficient of variation for each season are summarized in Table 2. In the hut, the air temperature remained relatively constant at on average 2°C warmer than outside, independent of season. Dominance score did not influence any of the behaviours ($p > 0.05$).

Table 2
Minimum and maximum air temperatures in the building in degrees Celsius and the coefficient of variation of the temperature throughout the day (24 h), by season.

	Autumn	Winter	Spring	Summer
T Min	10.7	8.8	7	14.4
T Max	15.9	11.9	16.6	26.2
CV	9 %	4.9 %	16.4 %	14.9 %

3.1. Contact behaviours influenced by season

The duration of lying in partial body contact differed between the seasons ($p < 0.001$), in which autumn had significantly higher average values between day and night (71 min; 2.7 times) than winter (31 min; 0.84 times) and summer (14 min; 0.5 times) but did not significantly differ from spring (56 min; 1.08 times) (Fig. 1). In summer, when the temperature was highest, the duration of lying in partial body contact was significantly lower than in other seasons, whereas the duration of lying in full body contact tended to be lower ($p = 0.06$) (Fig. 1). At the same time, in summer, the duration of lying with extremities in contact tended to be higher ($p = 0.06$) (Fig. 1). Pigs spent more time lying in body contact during the night (340 min out of 12 hours) than during the day (211 min) (for all 3 behaviours $p < 0.01$; Fig. 1). There was a season by daytime interaction for partial body contact ($p = 0.04$), with autumn day differing from summer and winter day, and autumn night from summer and winter night. Spring day differed from spring night, but only spring night differed from both summer day and summer night time and also from winter daytime (Fig. 1).

Agonistic and aggressive behaviour were influenced by season (both $p < 0.01$), with more agonistic behaviour and aggression in autumn as compared to winter and summer, but not spring (Fig. 2). The behaviours occurred almost exclusively during the day (both $p < 0.001$; Fig. 2). There was a season by daytime interaction for agonistic behaviour ($p = 0.006$) and aggressive behaviour ($p = 0.001$), driven by the greater frequency during autumn daytime (Fig. 2). Pregnancy did not significantly influence the variables related to the duration of body contact or the agonistic behaviours (all $p > 0.05$).

3.2. Contact behaviours uninfluenced by season

In line with our prediction, nosing body and nosing head occurred equally across the seasons ($p = 0.33$; $p = 0.94$, respectively). During the daytime, sows nosed each other's body on average 5.7 ± 0.63 times and heads 7.3 ± 0.50 times per 12 h, but hardly showed these behaviours during the night (nosing body: 0.4 ± 0.63; nosing head: 0.8 ± 0.50 times per 12 h) (both $p < 0.001$). Nosing body and nosing head showed no interaction between season and time of day ($p = 0.32$; $p = 0.88$, respectively). Nosing body, but not nosing head ($p > 0.05$), was shown significantly more by sows who were not pregnant (pregnant: 1.7 ± 0.69 times per 12 h; not pregnant: 4.3 ± 0.66 times per 12 h; $p = 0.02$).

3.3. Infrequently occurring behaviours

Allo-grooming, mounting, nudging and belly nosing occurred infrequently and mostly by specific individuals. Allo-grooming was shown by two pigs (average MDS of the two pigs per seasons: 2.95 and 11.17 in a range of −26.48–28.54 from across the dominance hierarchy), of which one showed substantially more allo-grooming (in total 40 out of 58 times shown by the same pig, average MDS = 2.95). Allo-grooming correlated with nosing body, nosing head and nudging, but not with mounting (Table 3). Mounting was shown only by 4 individuals (24 times in total) and correlated with nosing body, nosing head and nudging. Nudging, which occurred 160 times in total, correlated with nosing body and mounting, and not with nosing head (Table 3). The sum of mounting and nudging, reflecting sexual behaviour, was significantly less in pregnant females (pregnant: 0.15 ± 0.255 times per 12 h; not pregnant: 1.0 ± 0.242 times; $p = 0.02$). Belly nosing, expressed in the same manner as seen in young pigs, did also occur in the sub-adult pigs but only to a very limited extent (5 times in total, by two pigs), and was therefore not statistically analysed.

3.4. Lying orientation

Pigs mostly lay in nonparallel orientation (133 ± 88 min, SD; 3.2 ± 1.89 times on average per 12 h; 48 % of observations) or head-to-head (118 ± 41 min, SD; 2.8 ± 0.87 times; 43 % of observations), but clearly least in the head-to-tail orientation (24 ± min 15, SD; 0.8 ± 0.41 times; 9 % of observations). Season did not influence the percentage (based on durations) of lying nonparallel ($p=0.08$), head-to-head ($p = 0.20$) or head-to-tail ($p = 0.52$). The three lying orientations occurred with similar frequency during the day and night ($p > 0.05$). There was a season by daytime interaction for lying head-to-head ($p = 0.008$), but with the Bonferroni correction this did not result in significant post-hoc differences. Interestingly, pregnant pigs were lying less in head-to-tail orientation (pregnant: 5.7 ± 1.65 min; not pregnant: 11.3 ± 1.57 min; $p = 0.03$).

The frequency of lying orientations, which reflects the number of times pigs get up and lie down again from a certain lying orientation, showed a different pattern as compared to the percentages based on the durations. Season influenced the frequency of lying head-to-head ($p = 0.001$) and head-to-tail ($p = 0.01$) but not lying nonparallel ($p = 0.06$), with the frequency of lying down in a head-to-head and head-to-tail orientation being greater in autumn as compared to the other seasons (Fig. 3). The frequency was always greater during the day than during the night (all $p < 0.001$). There was a season by daytime interaction for the frequency of lying down head-to-tail ($p = 0.01$), whereby autumn day differed from all other time points except summer day. There was also an interaction for nonparallel orientation ($p = 0.002$), whereby autumn day differed from all other time points except spring and summer daytime; autumn night differed from summer day; and summer day differed from summer night and winter night (Fig. 3). Similar to the duration, pregnant pigs were lying less frequently head-to-tail (pregnant: 0.55 ± 0.125 times; not pregnant: 0.97 ± 0.119 times; $p = 0.03$).

Table 3
Spearman correlation between selected social behaviours, with the p-value between brackets.

Behaviour	Nosing head	Allo-grooming	Nudging	Mounting
Nosing body	0.67 (0.03)	0.68 (0.03)	0.83 (0.003)	0.89 (<0.001)
Nosing head		0.70 (0.02)	0.45 (0.19)	0.63 (0.05)
Allo-grooming			0.69 (0.03)	0.52 (0.13)
Nudging				0.71 (0.02)

3.5. Lying location

From the lying locations it becomes apparent that the group was lying down in one half of the pen, with the peak use around the hut, including in autumn when the hut was not yet established (Fig. 4). Interestingly, in winter pigs lay during the day more frequently outside the hut than inside. The coefficient of variation (CV) of the lying location was influenced by season ($p=0.04$), with a greater variation (CV) in

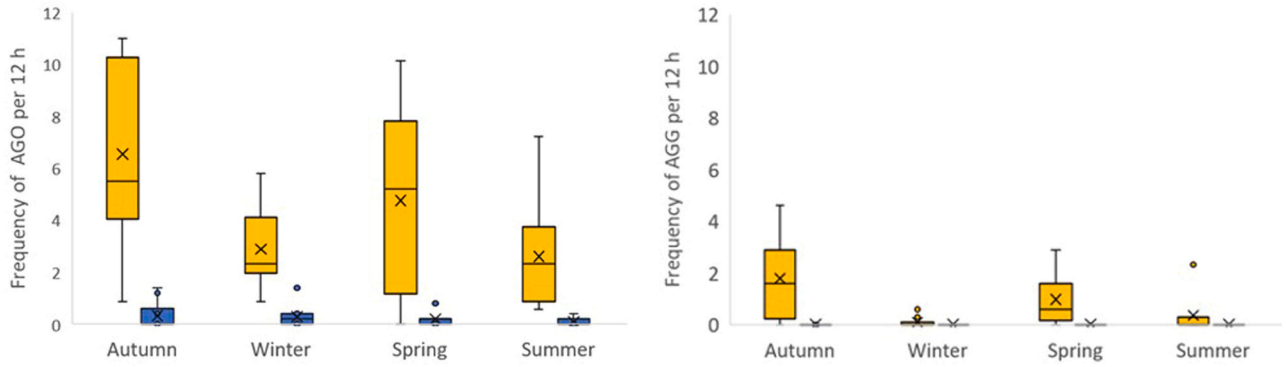

Fig. 2. Boxplot of frequencies per 12 h time block for agonistic behaviour (AGO; left) and aggressive behaviour (AGG; right) per season for day (in yellow) and night (in blue). Boxes range from 1st-3rd quartile while the inner line represents the median and the X the average. Whiskers below and above the boxes show the minimum observation above the lower fence (Q1 - 1.5 IQR) and the maximum observation below the upper fence (Q3 + 1.5 IQR). Outliers are represented as solid circles.

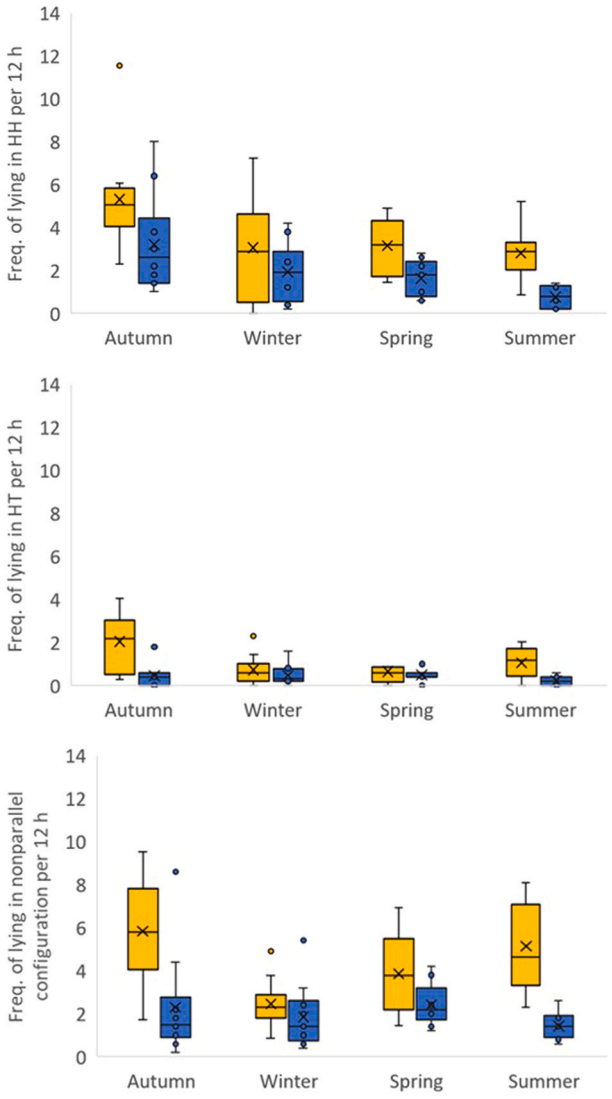

Fig. 3. Boxplot of frequencies of lying head-to-head (HH), head-to-tail (HT) and nonparallel per 12 h time block, by season and daytime (day: yellow; night: blue). Boxes range from 1st-3rd quartile while the inner line represents the median and the X the average. Whiskers below and above the boxes show the minimum observation above the lower fence (Q1 - 1.5 IQR) and the maximum observation below the upper fence (Q3 + 1.5 IQR). Outliers are represented as solid circles.

autumn (10.9 %) as compared to summer (7.5 %), but not compared to winter (8.4 %) or spring (9.1 %).

4. Discussion

From over 400 h of continuous day and night observations per animal, across four seasons, it becomes apparent that pigs spend a large part of their time in body contact, although most frequently only with a relatively small part of their body (extremities contact) when given the space to do so. As expected, they were lying least in body contact in summer, when the temperature was highest. However, significant effects of the season were only present for partial body contact; and the longest durations for partial contact were in autumn and not in winter. We further expected that affiliative social behaviours would remain constant throughout the year, which is indeed what we found.

4.1. Contact behaviours influenced by season

Pigs were lying less in surface contact with their body in summer, as seen from a lower duration of partial body contact, a lower tendency of lying in full body contact and a greater duration of lying with their extremities in contact. Summer had clearly the highest temperature, and the temperature inside the building reflected the outdoor temperature. Podder et al. (2022) also found that the general lying behaviour of non-pregnant sows (in India) halved in duration in summer (from approximately 400 to 200 min/12 h). In young pigs, the amount of full body contact also reduced at higher temperatures (Camerlink et al., 2022). Even in summer, with an average maximum temperature of 26°C, the pigs in our study kept in contact with the extremities of their body. As they had plenty of space to lie separately, on equally good resting locations, the continued contact suggests an affiliative need or purpose to maintain these subtle contacts regardless of external conditions. From an evolutionary perspective, remaining close together can increase the herd's vigilance of danger (e.g., noticing predators) and may thus serve a function (Fernández-Juricic et al., 2007), especially when resting.

Autumn stood out as the season with the most contact behaviour. Autumn had a similar average minimum and maximum temperature as spring, but in spring the temperatures varied more (higher coefficient of variation), with snow in the first observation week. It is therefore unclear why autumn differed in this manner. In autumn the hut was not yet built, and without the hut it may have been colder at the floor level, which could lead to pigs keeping in closer body contact. The hut may have created a warmer microclimate also outside the hut, as it was positioned between large doors to the outside and the resting area and thereby reduced the cold airflow. The access to the hut did not increase contact behaviour or clustering, which may be because of the potentially warmer microclimate just outside the hut.

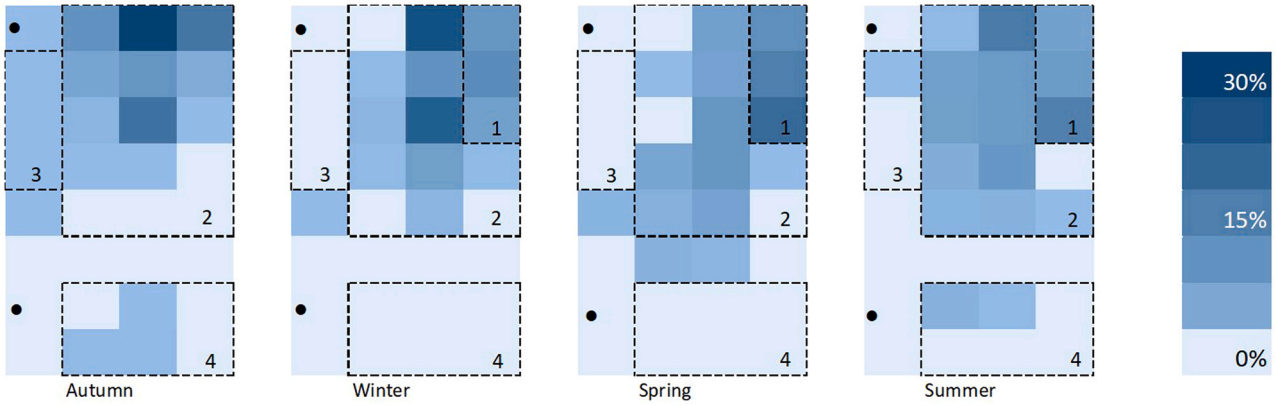

Fig. 4. Heat map of location usage across the 32 sections, with pigs lying down most frequently in the darkest coloured sections. The numbered boxes delimited by a dashed line represent: hut (1); bedding area (2); feeding area (3); dunging area (4). Black circles represent the two drinkers.

Lying in body contact occurs in pigs at least partly for thermoregulatory purposes (Huynh et al., 2005; Spoolder et al., 2012). As the breed that we used has a thick fat layer and is therefore better suited to colder temperatures than regular white breeds, they may not have adjusted their contact behaviour to seek warmth from each other in the winter observations due to this greater ability to tolerate cold temperatures.

The pigs spent more time lying in body contact at night than during the day, a result of less frequent posture changes during the night. When the duration for full and partial body contact and contact with the extremities is summed, it shows that the pigs were lying in contact for at least half of the 12 h of night observation, which corresponds with the lying duration in non-pregnant sows (400 mins / 12 h; Podder et al., 2022). For partial body contact there was a season by daytime interaction with more contact during the autumn and spring nights as compared to the days and nights in other seasons. This may be due to the greater temperature fluctuations in these seasons, especially in spring.

Agonistic behaviour and aggression were highest in autumn. While we may have expected an increase in agonistic behaviour in spring and summer due to the return of weaned sows to the group (Ewbank and Meese, 1971; O'Malley et al., 2022), the highest frequency of aggression was in autumn when the group was most stable. This shows that the return of sows to the herd after farrowing in our case did not result in long-lasting disruption in the social organization. The more frequent agonistic interactions may be related to the longer duration in body contact in autumn, as the closer proximity may result in a higher chance of conflict. Agonistic interactions were mostly around feeding. When starting the study (in autumn), the group had been subjected to floor feeding for approximately two months and were therefore familiar with the method. In spite of that, agonistic behaviour around feeding remained, which is common with floor feeding (Verdon et al., 2015). A season by daytime interaction for agonistic behaviour and aggression was driven by the higher aggression in autumn daytime. It has to be noted, though, that the frequency of agonistic behaviour and aggression was low, and aggression consisted only of unidirectional bites without any reciprocal fights.

4.2. Contact behaviours uninfluenced by season

Social nosing in pigs, such as nosing head and nosing body, has various putative functions such as recognition, communication and affiliation (Camerlink and Turner, 2013). In this study, social nosing was considered mostly as affiliative and communicative behaviour as the group was stable and therefore would not need to nose frequently for recognition (O'Malley et al., 2022). The frequency of social nosing occurred equally across the seasons, as we expected based on the non-seasonality of general communicative and affiliative behaviours. Nosing head and nosing body moderately correlated with each other but differed in how they related to other behaviours. Nosing body correlated strongly with nudging and mounting, which are behaviours related to reproduction (Pedersen, 2007; Hemsworth and Tilbrook, 2007) and coincide with increased social interest. Indeed, nudging and mounting (summed) occurred more frequently in the non-pregnant females, which likely were in heat. Nosing body correlated moderately with allo-grooming. Nosing head moderately correlated with allo-grooming and did not correlate significantly with nudging or mounting. It also did not depend on pregnancy. Nosing the head, which included here snout contact, therefore seems mostly related to affiliative behaviour. Overall, nosing the body appears to be a more general social behaviour whereas nosing the head appears to be more specific. The difference in the frequency of nosing behaviours between day and night is a logical consequence of the inactivity during the night time.

4.3. Infrequently occurring behaviours

Allo-grooming, mounting, nudging and belly nosing occurred infrequently. These behaviours were deliberately recorded separately during the observations, as for some behaviours it is not well-known whether they are merely witnessed infrequently due to the common use of scan sampling which is poor at detecting short-term behaviours, or whether these behaviours are truly infrequent.

This is especially the case for allo-grooming, which is not often observed in pigs. Allo-grooming or social grooming is reported sparingly in the literature of domestic pigs (Ewbank and Meese, 1971; Van Putten, 1978), where it contributes only a marginal percentage to the overall time budget in young pigs (Camerlink et al., 2022: 0.5 %). In the current study, only two out of ten individuals performed allo-grooming. Given that the observations were done in an age group where allo-grooming is expected to occur (from 8 weeks of age: Meynhardt, 1982) and over a substantial number of hours (406 h), we can confirm that allo-grooming is present but indeed an infrequent behaviour which seems to be heavily influenced by an individuals' propensity to allo-groom. The correlations with other behaviours reconfirm that allo-grooming has an affiliative role unrelated to sexual behaviour. Allo-grooming was performed by pigs from across the dominance hierarchy and therefore the results confirm earlier work indicating the absence of a link between allo-grooming and dominance ranks in pigs (Camerlink and Turner, 2013). As the group had plenty of straw and other materials to chew on, allo-grooming also does not seem to be a redirected behaviour, as suggested by Van Putten (1978).

Mounting and nudging, both as part of the sexual behavioural repertoire, also occurred infrequently and mostly in non-pregnant pigs, likely in relation to being in heat. However, while in nature sows have breeding seasons (Mauget, 1982), wild boar possess plasticity in their reproductive timing (Brogi et al., 2022), with their cycle adapting to external conditions such as the photoperiod (Brogi et al., 2022). This natural cycle is suppressed under farm conditions due to the much earlier removal of piglets, with weaning inducing the next heat in the sow (Love et al., 1993), as well as due to the staged presence of a boar to stimulate heat.

The reason for the occasional performance of belly nosing is unclear. The behaviour resembled belly nosing as described in young weaned pigs (Widowski et al., 2008), in which it is related to the innate need at this age to massage the sow's udder to obtain milk (Torrey and Widowski, 2006). As it does not commonly occur in adult animals, we do not draw any conclusions on the occurrence of this behaviour or what its intention may have been.

4.4. Lying orientation and location

Pigs were lying mostly head-to-head or nonparallel to each other. Considering the role of social nosing of the head in affiliative behaviour, resting in a head-to-head configuration contributes to their affiliative relationships better than a head-to-tail orientation. Lying head-to-tail occurred clearly least, which has also been observed previously in piglets (Camerlink et al., 2022).

The percentage of occasions in which pigs adopted the different orientations remained the same between day and night, however, during the day pigs were more active as compared to the night and changed position more frequently. Season did not influence the duration of each lying orientation, but did affect the frequency. Head-to-head and head-to-tail frequencies were almost double in autumn as compared to the three other seasons, which may be due to the longer durations in body contact in autumn as discussed above. The higher frequencies in autumn also resulted in a daytime by season interaction. The longer duration and greater frequency of lying head-to-tail in non-pregnant females was unexpected, and might relate to a greater interest in ano-genital nosing to assess each other's reproductive status (Pedersen, 2007).

The observations on lying location showed that the pigs kept largely separate functional areas (resting area, feeding area, toilet area; Fig. 4) which is their natural behaviour when given the space allowance to do so (Petherick, 1983; Spoolder et al., 2012). The native breed appeared to be well suited to the climatic conditions, as in winter their preferred

resting areas were not predominantly in the warmer hut area.

The coefficient of variation of the lying location was greater in autumn than in summer, which may relate to the longer durations of lying down. We expected pigs to occupy more locations as the temperatures increased, as reported in previous studies (e.g. Hillmann et al., 2004). This seems to be the case from Fig. 4, however the lowest variation in location use was in summer, which may indicate that individual pigs varied little in their location use but as a group did spread out more. The CV also showed that pigs varied in where they were lying down without a clear preferred lying location. However, the sections as determined in this study were only 4 m^2 (fitting approximately two sows) and it could be that preferred resting locations or areas are present when considering larger sections.

4.5. Study limitations

The overarching aim of this study was to determine in detail the occurrence of pigs' contact behaviour, which could then serve to determine the right observation methods for future larger scale studies or automated behaviour analysis. We were a priori aware that the small sample size of one group would be a limitation in extrapolating the results of the current study to other populations, but deliberately chose a small study sample in order to obtain the most detailed data. The amount of hours of observation (406 h per sow) and the detail of the ethogram would not have been feasible on a large number of groups, or on multiple groups per season. Moreover, farms that offer a large space allowance typically have only one or few comparable groups of sows.

Temperature was recorded to reflect differences between the seasons. However, this did not explain the behavioural differences in autumn. A main difference in autumn was the absence of the hut. While the warmer temperature in the hut seemed to have limited effect on the location usage, the hut may have formed a barrier against draft from the uninsulated front door. Measuring microclimates, and including air velocity and humidity, could have been of use in explaining our results, as air velocity in combination with temperature can affect contact behaviour and lying position of pigs (Olczak et al., 2015). Due to technical errors, humidity was not recorded in each season.

In the current set-up, season naturally confounded with age and subsequently also with body weight. In autumn, pigs were younger and lighter (weighing ~100 kg) than in spring, by which point they had approximately doubled in weight. Both age and body weight can influence lying behaviour (Blackshaw and Blackshaw, 1994; Hillmann et al., 2004). However, as the pigs remained in a similar life phase (sub-adult), and had a body weight range in which their thermal neutral zone remained similar, we expect any potential influences of age or body weight to be minor. An additional consideration hereby is the breed (Puławska), which is slower growing and has more fat than typical commercial breeds, and therefore at a weight of 100 kg will be around 2–3 months older than commercial breeds and have a well-insulating fat layer. Studying additional groups while starting from different seasons would avoid the confound, but given the aforementioned considerations we believe this would not have added substantially to answering the research question, while limiting the ability to collect qualitatively stronger data for one group.

Following a group for two full weeks per season means that there is a high chance of females being in heat in the observation days (given their 21-day fertility cycle). Sexual behaviour, most notably mounting, was more frequent in females who were not pregnant and may therefore change results as compared to a group of pregnant sows or pre-pubertal gilts. However, the short-lived sexual behaviour of gilts in heat (typically 48–80 h (Eliasson, 1989)) occurred infrequently (only 24 times mounting in 406 h) and probably therefore had limited impact on the longer lasting observations, which emphasizes the strength of doing behavioural observations over a sustained time frame.

Further, it has to be noted that we recorded lying in contact and not lying separate from others, as previous research showed that lying separated occurred only 9 % of the time (Camerlink et al., 2022). Since only active lying down was scored (following Goumon et al., 2020), the real duration of lying in body contact will have been more than that recorded here. The reason for scoring active lying down rather than all contact, was to assess the directionality of the behaviour as part of social preferences, with active lying down reflecting the individual's social choice for another animal (Goumon et al., 2020).

5. Conclusions

Detailed observations of contact behaviours in pigs, recorded during day and nighttime across four seasons, showed that social, mostly affiliative, behaviours occur regardless of season and temperature. Body contact did vary between the seasons, with less body contact in summer when the temperature was highest. This shows that spatial proximity is affected by external conditions such as temperature, which may have consequences when using spatial proximity as a measure of social relationships. Pigs kept largely separate functional areas and varied in where they lay down, without a clear preferred lying location between seasons.

Social nosing behaviour remained constant throughout the year, as we expected based on the non-seasonality of general communicative and affiliative behaviours.

This study provided deeper insight into subtle social behaviours such as nosing the head and body and allo-grooming.

CRediT authorship contribution statement

Simon P. Turner: Writing – review & editing, Supervision, Funding acquisition. **Irene Camerlink:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization. **Piero Seddaiu:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Andersen, I.L., Bøe, K.E., Kristiansen, A.L., 1999. The influence of different feeding arrangements and food type on competition at feeding in pregnant sows. Appl. Anim. Behav. Sci. *65* (2), 91–104.

Andersen, I.L., Roussel, S., Ropstad, E., Braastad, B.O., Steinheim, G., Janczak, A.M., Bøe, K.E., 2008. Social instability increases aggression in groups of dairy goats, but with minor consequences for the goats' growth, kid production and development. Appl. Anim. Behav. Sci. *114* (1-2), 132–148.

Blackshaw, J.K., Blackshaw, A.W., 1994. Shade-seeking and lying behaviour in pigs of mixed sex and age, with access to outside pens. Appl. Anim. Behav. Sci. *39* (3-4), 249–257.

Brogi, R., Merli, E., Grignolio, S., Chirichella, R., Bottero, E., Apollonio, M., 2022. It is time to mate: population-level plasticity of wild boar reproductive timing and synchrony in a changing environment. Curr. Zool. *68* (4), 371–380.

Camerlink, I., Bijma, P., Kemp, B., Bolhuis, J.E., 2012. Relationship between growth rate and oral manipulation, social nosing, and aggression in finishing pigs. Appl. Anim. Behav. Sci. *142* (1-2), 11–17.

Camerlink, I., Scheck, K., Cadman, T., Rault, J.L., 2022. Lying in spatial proximity and active social behaviours capture different information when analysed at group level in indoor-housed pigs. Appl. Anim. Behav. Sci. 246, 105540.

Camerlink, I., Turner, S.P., 2013. The pig's nose and its role in dominance relationships and harmful behaviour. Appl. Anim. Behav. Sci. *145* (3-4), 84–91.

Camerlink, I., Turner, S.P., Ursinus, W.W., Reimert, I., Bolhuis, J.E., 2014. Aggression and affiliation during social conflict in pigs. PloS One *9* (11), e113502.

Cascio, C.J., Moore, D., McGlone, F., 2019. Social touch and human development. Dev. Cogn. Neurosci. *35*, 5–11.
Champagne, F., Diorio, J., Sharma, S., Meaney, M.J., 2001. Naturally occurring variations in maternal behavior in the rat are associated with differences in estrogen-inducible central oxytocin receptors. Proc. Natl. Acad. Sci. *98* (22), 12736–12741.
Chua, B., Coenen, E., Van Delen, J., Weary, D.M., 2002. Effects of pair versus individual housing on the behavior and performance of dairy calves. J. Dairy Sci. *85* (2), 360–364.
Dunbar, R.I., 1991. Functional significance of social grooming in primates. Folia Primatol. *57* (3), 121–131.
Ekkel, E.D., Spoolder, H.A., Hulsegge, I., Hopster, H., 2003. Lying characteristics as determinants for space requirements in pigs. Appl. Anim. Behav. Sci. *80* (1), 19–30.
Eliasson, L., 1989. A study on puberty and oestrus in gilts. J. Vet. Med. Ser. A *36* (1-10), 46–54.
Ewbank, R., Meese, G.B., 1971. Aggressive behaviour in groups of domesticated pigs on removal and return of individuals. Anim. Sci. *13* (4), 685–693.
Fernández-Juricic, E., Beauchamp, G., Bastain, B., 2007. Group-size and distance-to-neighbour effects on feeding and vigilance in brown-headed cowbirds. Anim. Behav. *73* (5), 771–778.
Fish, E.W., Shahrokh, D., Bagot, R., Caldji, C., Bredy, T., Szyf, M., Meaney, M.J., 2004. Epigenetic programming of stress responses through variations in maternal care. Ann. N. Y. Acad. Sci. *1036* (1), 167–180.
Gilbert, C., McCafferty, D., Le Maho, Y., Martrette, J.M., Giroud, S., Blanc, S., Ancel, A., 2010. One for all and all for one: the energetic benefits of huddling in endotherms. Biol. Rev. *85* (3), 545–569.
Goumon, S., Illmann, G., Leszkowová, I., Dostalová, A., Cantor, M., 2020. Dyadic affiliative preferences in a stable group of domestic pigs. Appl. Anim. Behav. Sci. 230, 105045.
Grandi, L.C., Ishida, H., 2015. The physiological effect of human grooming on the heart rate and the heart rate variability of laboratory non-human primates: a pilot study in male rhesus monkeys. Front. Vet. Sci. 2, 50.
Hemsworth, P.H., Tilbrook, A.J., 2007. Sexual behavior of male pigs. Horm. Behav. 52 (1), 39-44.105045.
Herpin, P., Damon, M., Le Dividich, J., 2002. Development of thermoregulation and neonatal survival in pigs. Livest. Prod. Sci. *78* (1), 25–45.
Herskin, M.S., Jensen, K.H., 2000. Effects of different degrees of social isolation on the behaviour of weaned piglets kept for experimental purposes. Anim. Welf. *9* (3), 237–249.
Hertenstein, M.J., Keltner, D., App, B., Bulleit, B.A., Jaskolka, A.R., 2006. Touch communicates distinct emotions. Emotion *6* (3), 528.
Hillmann, E., Mayer, C., Schrader, L., 2004. Lying behaviour and adrenocortical response as indicators of the thermal tolerance of pigs of different weights. Anim. Welf. *13* (3), 329–335.
Huynh, T.T.T., Aarnink, A.J.A., Gerrits, W.J.J., Heetkamp, M.J.H., Canh, T.T., Spoolder, H.A.M., Verstegen, M.W.A., 2005. Thermal behaviour of growing pigs in response to high temperature and humidity. Appl. Anim. Behav. Sci. *91* (1-2), 1–16.
Ieraci, A., Mallei, A., Popoli, M., 2016. Social isolation stress induces anxious-depressive-like behavior and alterations of neuroplasticity-related genes in adult male mice. Neural Plast. 2016.
Jablonski, N.G., 2021. Social and affective touch in primates and its role of skin in the evolution of social cohesion. Neuroscience *464*, 117–125.
Jarvis, S., D'Eath, R.B., Robson, S.K., Lawrence, A.B., 2006. The effect of confinement during lactation on the hypothalamic–pituitary–adrenal axis and behavior of primiparous sows. Physiol. Behav. *87* (2), 345–352.
Jørgensen, G.H.M., Andersen, I.L., Bøe, K.E., 2009. The effect of different pen partition configurations on the behaviour of sheep. Appl. Anim. Behav. Sci. *119* (1-2), 66–70.
Jowett, S.L., Barker, Z.E., Amory, J.R., 2023. Preferential associations in an unstable social network: applying social network analysis to a dynamic sow herd. Front. Vet. Sci. *10*, 1166632.
Kutsukake, N., Castles, D.L., 2001. Reconciliation and variation in post-conflict stress in Japanese macaques (Macaca fuscata fuscata): testing the integrated hypothesis. Anim. Cogn. *4*, 259–268.
Lehmann, J., Korstjens, A.H., Dunbar, R.I., 2007. Group size, grooming and social cohesion in primates. Anim. Behav. *74* (6), 1617–1629.
Love, R.J., Evans, G., Klupiec, C., 1993. Seasonal effects on fertility in gilts and sows. J. Reprod. Fertil. 191–1911.
Mauget, R., 1982. Seasonality of reproduction in the wild boar. Control pig Reprod. 509–526.
Mellor, D.J., Beausoleil, N.J., 2015. Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states. Anim. Welf. *24* (3), 241–253.
Meynhardt, H., 1982. Schwarzwildreport. Mein Leben Unter Wildschweinen. Neumann-Neudamm, Germany, Melsungen.
Miller, K., Wood-Gush, D.G.M., 1991. Some effects of housing on the social behaviour of dairy cows. Anim. Sci. *53* (3), 271–278.
O'Malley, C.I., Steibel, J.P., Bates, R.O., Ernst, C.W., Siegford, J.M., 2022. The social life of pigs: changes in affiliative and agonistic behaviors following mixing. Animals *12* (2), 206.
Olczak, K., Nowicki, J., Klocek, C., 2015. Pig behaviour in relation to weather conditions–a review. Ann. Anim. Sci. *15* (3), 601–610.
Pedersen, L.J., 2007. Sexual behaviour in female pigs. Horm. Behav. *52* (1), 64–69.
Petersen, V., Recén, B., Vestergaard, K., 1990. Behaviour of sows and piglets during farrowing under free-range conditions. Appl. Anim. Behav. Sci. *26* (1-2), 169–179.
Petherick, J.C., 1983. A biological basis for the design of space in livestock housing. Farm Anim. Hous. Welf. *24*, 15–343.
Podder, M., Bera, S., Naskar, S., Sahu, D., Mukherjee, J., Patra, A.K., 2022. Physiological, blood-biochemical and behavioural changes of Ghoongroo pigs in seasonal heat stress of a hot-humid tropical environment. Int. J. Biometeorol. *66* (7), 1349–1364.
Romero, T., Castellanos, M.A., De Waal, F.B., 2010. Consolation as possible expression of sympathetic concern among chimpanzees. Proc. Natl. Acad. Sci. *107* (27), 12110–12115.
Sánchez-Villagra, M.R., Pope, T.R., Salas, V., 1998. Relation of intergroup variation in allogrooming to group social structure and ectoparasite loads in red howlers (Alouatta seniculus). Int. J. Primatol. *19*, 473–491.
Silk, J.B., Altmann, J., Alberts, S.C., 2006. Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. *61*, 183–195.
Spoolder, H.A., Aarnink, A.A., Vermeer, H.M., van Riel, J., Edwards, S.A., 2012. Effect of increasing temperature on space requirements of group housed finishing pigs. Appl. Anim. Behav. Sci. *138* (3-4), 229–239.
Stanged, G., Jensen, P., 1991. Behaviour of semi-naturally kept sows and piglets (except suckling) during 10 days postpartum. Appl. Anim. Behav. Sci. *31* (3-4), 211–227.
Thomas, P.A., Kim, S., 2021. Lost touch? Implications of physical touch for physical health. J. Gerontol.: Ser. B 76 (3), e111–e115.
Torrey, S., Widowski, T.M., 2006. Is belly nosing redirected suckling behaviour? Appl. Anim. Behav. Sci. 101 (3-4), 288–304.
Van Putten, G., 1978. Comfort behaviour in pigs: informative for their well-being. In The Ethology and Ethics of Farm. Animal Production: Proceedings of the 28th Annual Meeting. Birkhäuser, Basel, pp. 70–76.
Verdon, M., Hansen, C.F., Rault, J.L., Jongman, E., Hansen, L.U., Plush, K., Hemsworth, P.H., 2015. Effects of group housing on sow welfare: a review. J. Anim. Sci. 93 (5), 1999–2017.
Vieira, A.D.P., Von Keyserlingk, M.A.G., Weary, D.M., 2010. Effects of pair versus single housing on performance and behavior of dairy calves before and after weaning from milk. J. Dairy Sci. 93 (7), 3079–3085.
Weiss, I.C., Pryce, C.R., Jongen-Rêlo, A.L., Nanz-Bahr, N.I., Feldon, J., 2004. Effect of social isolation on stress-related behavioural and neuroendocrine state in the rat. Behav. Brain Res. 152 (2), 279–295.
Widowski, T.M., Torrey, S., Bench, C.J., Gonyou, H.W., 2008. Development of ingestive behaviour and the relationship to belly nosing in early-weaned piglets. Appl. Anim. Behav. Sci. 110 (1-2), 109–127.
Yin, G., Liu, H., Li, X., Quan, D., Bao, J., 2016. Effect of farrowing environment on behaviour and physiology of primiparous sows with 35-day lactation. Intern J. Appl. Res. Vet. Med. 14 (2), 159–169.

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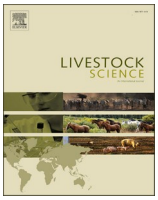

Long-term social preferences in a group of sub-adult female pigs

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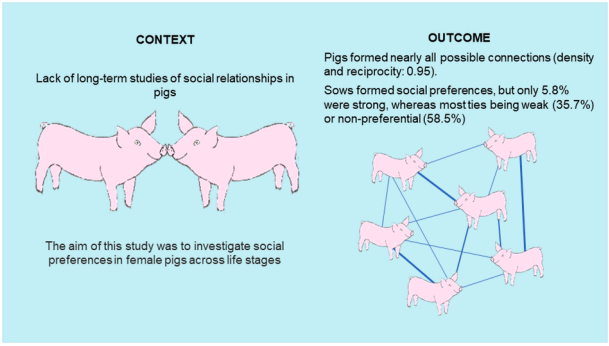
HIGHLIGHTS

- Pigs' social preferences were studied across four seasons.
- Social network analysis showed high cohesion but weak centralization.
- Strong social preferences were rare, with most ties being weak or non-preferential.
- Preferences persisted at most two seasons, with modest correlations across seasons.
- Transitions linked to reproductive status may influence sociality in pigs.

GRAPHICAL ABSTRACT



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Group cohesion

ABSTRACT

Social relationships in farm animals, including pigs, have become a focus of research, yet long-term studies are scarce. Pigs, being highly social animals, offer an excellent model to explore social preferences over time. This study aimed to investigate social preferences in female pigs across life stages by observing a group of ten gilts over one year, with each season serving as an assessment point. Social interactions (allogrooming, snout-body, and snout-head contact) were recorded through live and video observations, totaling 396 h per animal. Social Network Analysis (SNA) assessed group cohesion using measures of density, reciprocity, and degree centralization. Monte Carlo simulations, half-weight association index (HWI) and the Quadratic Assignment Procedure (QAP) were used to evaluate social preferences and their recurrence across seasons. Results showed high density (0.95) and reciprocity, with weak centralization (in-degree 0.19, out-degree 0.27), indicating uniform distribution of social interactions. On average across the four seasons, 5.8 % of connections were strong, 35.7 % weak, and 58.5 % non-preferential. Social preferences correlated modestly between autumn and winter, but not with summer and spring. This study confirms previous findings that only a small proportion of pigs form non-random associations within a group. Social preferences lasted for a maximum of two seasons, likely influenced by pregnancy and transitions from gilt to adult sow, which resulted in temporary withdrawal from the group.

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1. Introduction

Social preferences refer to the selective interaction with certain individuals over others within the same social group (Hinde, 1976). Within the context of affiliative behaviours, the formation of social preferences can provide advantages to individuals and to the social group in terms of increased group cohesion and reduced conflict, which can result in increased welfare and fitness (Silk et al., 2003; Weidt et al., 2008). Conversely, the disruption or prevention of the expression of social preferences can lead to psychological stress (Fone and Porkess, 2008). While relatively short-term social preferences have been studied across species (e.g., Gero et al., 2005; Muller et al., 2018; Perryman et al., 2019), in particular primates (e.g., Silk et al., 2006; Schülke et al., 2013; Bray and Gilby, 2020), there is limited research on how social preferences change over time and across different life stages.

Under commercial farm conditions, animals are commonly kept in unnatural group sizes and group compositions (e.g., large homogeneous groups). In spite of this, short-term social preferences exist in cattle (e.g., McLennan, 2013; Gutmann et al., 2015; Ozella et al., 2023), sheep (Ozella et al., 2022) and pigs (Durrell et al., 2004; Goumon et al., 2020), amongst other species. To facilitate farm management, group compositions may change several times during a production cycle, especially during weaning and in dynamic social groups (pigs: Jowett et al., 2023). In pigs, regrouping may disrupt existing social preferences and forces animals to establish new dominance relationships, often leading to increased aggression and stress (Lee et al., 2022). It may take at least 3 weeks before a newly established group of pigs has reached social stability (Meese and Ewbank, 1973; Prevolnik Povše et al., 2021). However, given the absence of long-term studies, it is generally unknown whether farm species form long-term social preferences and how disruption of such relationships may impact the group or individual animal welfare.

Previous studies reported that wild boar (Podgórski et al., 2014), as well as commercially housed pigs (Durrell et al., 2004; Goumon et al., 2020), form social preferences. In wild boar, most of the animals do not preferentially associate (only 20–34 % of the dyads; Podgórski et al., 2014). From those who did associate, sisters formed long-term social bonds, but males maintained only short-lived relationships which were not kin-directed, thereby emphasizing the matrilineal social structure. In domestic pigs, similar to wild boar, short-term preferential associations are typically weak, with stronger association only between a few individuals (Goumon et al., 2020; Camerlink et al., 2023). Although these studies were conducted under different conditions, namely wild populations in natural environments and pigs in semi-commercial housing, the consistency of results suggests that weak and selective social preferences may be a general characteristic of pig social behaviour. However, there is currently a lack of knowledge on why and with whom pigs preferentially interact, and whether these preferences are stable across time and life stages.

The primary objective of this study was to determine whether domestic pigs form long-term affiliative social preferences. Specifically, we investigated whether pigs maintain consistent social preferences across different seasons of the year and if the number and stability of these preferences relate to group-level sociability, as indicated by density and reciprocity of the social networks. We hypothesized that female pigs would show stable social preferences across time. In addition, we hypothesized that, despite being kept under large space allowance, the stable group would maintain high levels of reciprocity and density of the social networks, indicating strong group cohesion.

2. Methods

2.1. Animals and housing

Ten sub-adult female pigs (gilts) of the Puławska breed were studied at the pig research facility of the Institute of Genetics and Animal Biotechnology of the Polish Academy of Sciences, Jastrzębiec, Poland. The gilts were purchased from a breeder, who weaned piglets at 4–5 weeks of age and then reared pigs in groups of approximately 30 (several litters together), until they were ~50 kg. Thereafter pigs were randomly allocated to groups of ten, and from 70 kg the males and females were separated. At 6 months of age, ten gilts were selected from across three different rearing pens (2–4 pigs per pen) based on physical appearance (clinical health, leg conformation and body size) and behaviour at selection (inquisitiveness and response to humans). By chance, seven of the selected gilts were full-sibs (sisters of the same litter), two were full-sibs from another litter, and one was a half-sib (same sire) of the seven sisters. Although kinship may potentially influence social preferences, it was not treated as a separate factor in our analysis because seven of the ten pigs were closely related, leaving insufficient variation to evaluate its effect.

Pigs were weighed and transported to the research facility and housed as one group indoors in an enclosure of 16.0 × 6.75 m, providing a total space allowance of 108.5 m^2. The area had a solid concrete floor with deep straw bedding. Two bales of fresh straw (ca. 500 kg each) were provided once a week after cleaning, and daily 10 kg of fresh straw was added. A enrichment (aside from straw bedding), pigs had a brush fixed against the wall and a chain hanging on the fence. From winter onwards, a covered hut (dimensions: 6.0 × 2.0 × 1.5 m; 1.2 m2 / pig) made from wood was provided within the barn for the pigs to stay warm (Fig.1). Pigs were fed twice a day by floor feeding (at 09:00 and 15:00 h). Fine-gained dry commercial sow feed (total 3.2 kg per sow per day, 10.26 MJ/kg) was mixed with water, oil and lysine (wet weight 6.4 kg per sow) and delivered in a long line on the floor to provide access to all pigs. Water was provided ad libitum through two drinkers. The building was naturally ventilated (unheated) and the ambient temperature was recorded every hour using a temperature logger (Eliotech RC-5). Due to technical issues, humidity was not recorded in every season, and was therefore not included in the study.

As the pigs were observed across a year, some gilts left the group temporarily for farrowing. They were relocated to the farrowing pens one week before the expected parturition date and returned to the group approximately six weeks later, when they were weaned from their piglets at 5 weeks post-farrowing. The group consisted of ten individuals in autumn and winter, while in spring and summer there were nine individuals present. The social network analysis and association matrices were constructed based on the actual number of animals present in each season. Sows were reunited in the group by temporarily increasing the space allowance and under constant supervision from the researchers. The pigs were monitored daily for their health and provided with appropriate veterinary care whenever necessary. The study was observational and therefore did not require ethical approval according to the national guidelines (non-invasive studies are not considered by the local ethical committee).

2.2. Behavioural observations

The pigs were 8 months old at the time of the first observations in October 2022, and 16 months at the last observations in June 2023. They were individually recognized by their unique coat patterns and by a mark drawn on their back with animal marking crayon (Raidex). Markings were redone daily at least 30 min before the start of the observations. The pigs were accustomed to being marked and would remain idle or approach the person upon marking. Behaviours were scored using the ethogram described in Table 1, while noting the actor and recipient of the behaviour. Behaviour was recorded through continuous observation, using the Animal Behaviour Pro App, version 1.2 (University of Kent, Canterbury, UK), installed on an iPad. Due to the large space allowance, calmness of the pigs and clear individual markings, synchronous observation of up to ten pigs was possible. Pigs were observed live and from video for 99 h per season divided across 10 days, spread over two weeks of observation. In total, 39 h daytime and 60 h

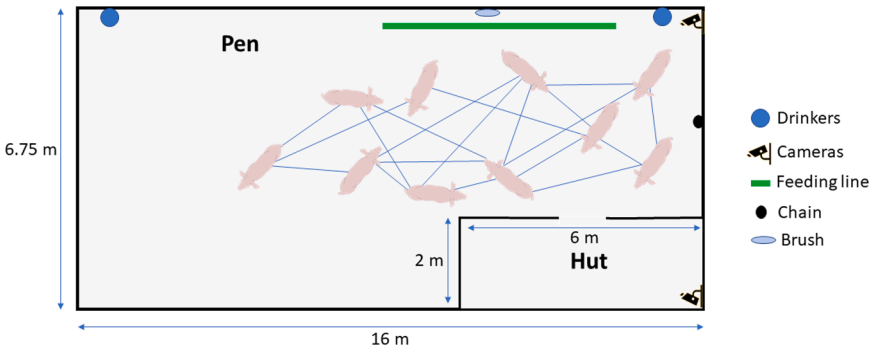

Fig. 1. Graphical representation of the study area.

Table 1
Ethogram for social behaviours during daytime (live observation) and nighttime (video observation).

Behaviour	Description
Snout-body contact	The focal animal touches the body of the recipient with its nose disc, excluding the head.
Snout-head contact	The focal animal touches the recipient's head with its nose disc; which can include the snout; excludes allogrooming.
Allogrooming	The focal animal gently nibbles or licks the body or head of the recipient while not causing acute skin damage. Excludes 'belly nosing'.

nighttime observations were collected in each season. Due to the different number of observation hours, the frequencies were converted to 12-hour averages, so that the behaviours during the day and night were both expressed as average per 12-hour time block. The resulting daytime and nighttime frequencies were then summed, in order to obtain a value per individual for each season.

During the daytime, observations were done live by one trained observer, who observed in blocks of 2 - 2.5 h between 09:30 and 17:00 h, with not more than five hours a day. During the nighttime, behaviours were recorded on video. Four orange LED tubes (126 cm length) were placed above the enclosure to guarantee visibility at night whilst not disrupting the pigs with white light. Two wide angle sports camera (AKASO EK7000) were placed to record the full enclosure, one in the main area and one inside the hut (Fig.1). Continuous recording began at 18.30 h and lasted for 12 h. Nighttime observations were obtained from five nights per season, balanced across the observation weeks. Videos were analyzed using Windows Media Player (version 11) while scoring the behaviour manually in Excel. Videos were analysed by the same observer as the live observations, using the same ethogram as during daytime.

2.3. Social network analysis

Social network analysis (SNA) is a method to assess the structure of relationships in a social group. This approach examines individuals and groups in the context of interactions (called 'ties' or 'edges') between group members (represented as 'nodes') (Wey et al., 2008). SNA allows the study of how social relationships change over time, thus providing insights into the stability and dynamics of social groups. This can be particularly important for understanding how pigs form and maintain social bonds. In this study, we analyzed how the social network of affiliative behaviours (snout-body, snout-head and allogrooming; Table 1) evolves over time by looking at changes in network properties using the measures of density, reciprocity and degree centrality. These measures allow evaluation of the stability, cohesion and sociality of the group over a long period of time. Stable social networks tend to have consistent density, high reciprocity, and stable centrality measures. Here, we used SNA to verify if these measures relate to the social preferences and how these change in the long term.

Density is a measure of how well individuals are connected within a group and facilitates the examination of changes over time within the same group of animals across different periods (Büttner et al., 2020). Density is the ratio between the number of actual observed connections and the number of potential connections given a group of individuals of the same size. The value ranges from 0 to 1, whereby 1 indicates that all potential connections were actually observed (i.e., every animal interacted with every other animal).

Reciprocity refers to the proportion of connections within the network that were reciprocal rather than uni-directional. Reciprocity is a crucial aspect of a social structure, as it can refer to both the balance and the hierarchy of a network. A network composed predominantly of reciprocal affiliative connections shows greater stability than one composed mostly of non-reciprocal connections (Hanneman and Riddle, 2005). Reciprocity has a value between 0 and 1 and represents the proportion of dyads in which the behaviour flowed in both directions relative to the total number of dyads in the group. This value will be 0 if none of the connections are mutual and 1 if all connections are mutual.

Degree is a measure of the centrality of an individual and quantifies the number of group members an individual interacted with (Farine and Whitehead, 2015). Additionally, the disparity in degree between group members can be quantified as a group-level metric, termed degree centralization. *In-degree centralization* is a group-level measure and quantifies the extent to which a single individual is the primary recipient of interactions in the group, whereas *out-degree centralization* measures the extent to which an individual is the primary initiator of interactions. Hence, in- and out-degree centralization reflect the heterogeneity in sociability within the group. It ranges from 0 (maximum homogeneity) to 1 (maximum heterogeneity).

As this study focused on the nature and stability of the social network over a relatively long period of time, we calculated measures at group level (density, reciprocity, in- and out-degree centralization) across the four seasons to observe their trends. Stable networks would likely exhibit relatively smooth and predictable temporal dynamics. For social network analysis we created a matrix of interactions for each season, where the columns and lines represented individual subjects, and the intersections of the lines with the columns represented the frequency of interactions between those two individuals. Frequencies of snout-body contact, snout-head contact and allogrooming (Table 1), as well as during day and night, were summed, resulting in one matrix for each season. We then calculated density, reciprocity, out-degree centralization and in-degree centralization using the Whole-Network measures function in UCINET software (version 6 for Windows) (Borgatti et al., 2002).

2.4. Statistical analysis

We analyzed social preferences of each pig in each season using the same matrices of interaction used for the SNA analysis described above.

All the statistical analyses were conducted in UCINET (version 6) or R (version 4.3.2).

To evaluate whether the frequencies of affiliative interactions were more variable between individuals than expected by chance, we conducted a Monte Carlo test for the interaction rates matrix of each season (following Goumon et al., 2020). The Monte Carlo method is a computational technique that uses random sampling to obtain numerical results. In this study, the Monte Carlo method created a theoretical distribution of means and CVs of interaction rates by permuting the data 1000 times. We considered that social preferences were likely to exist when the CV of the observed interaction data was higher than the mean CV of all permuted replicates. In this case, a high CV would indicate high heterogeneity in the interaction rate. Significance was established when the observed CV was outside the 95 % confidence interval of the distribution of CVs created by the Monte Carlo test. Subsequently, preferential associations were analyzed by using frequency matrices. The half-weight association index (HWI: Cairns and Schwager, 1987, Ginsberg and Young, 1992) was calculated with the equation: $HWI = x/(na + nb)/2$; where x is the number of times individual a and individual b interacted with each other in the observation period; na is the number of individual a interactions in the same period; and nb is the number of individual b interactions in the same period. The HWI quantifies the strength of association between pairs of individuals based on their interaction frequencies, taking into account both the number of times two individuals interact with each other and the number of times they interact with other individuals. Social preferences were classified based on the average HWI as a threshold value. Preferences were classified as strong when the value obtained was greater than twice the average HWI; weak when it was equal to or lower than twice the average HWI; and classified as no association when the value was lower than the average HWI. This threshold value was chosen because it is approximately twice the expected value than if associations were completely random, and has been used previously in similar studies (as in Durrell et al., 2004, Gero et al., 2005, Li et al., 2018, Goumon et al., 2020). For each season, a matrix of HWI was created. The rows and columns of the matrix represented individual pigs, and the cells contained the HWI values between the pigs corresponding to the respective row and column. We then correlated the four matrices to evaluate repeatability of association strength using the Quadratic Assignment Procedure (QAP) with 5000 permutations. QAP is a measure of correlation and, with this test, we evaluated whether preferential associations repeated across the four seasons. The number of permutations was based on Li et al. (2018) and corresponds to the UCINET default setting, which balances robust significance testing with computational efficiency.

As one pig was absent in spring and another in summer, all dyads involving those individual in that specific season were excluded from the correlation with other seasons. Therefore, correlations were based on the overlapping dyads present in both matrices.

3. Results

3.1. Social network metrics across seasons

Density and reciprocity showed that group cohesion and sociality were highly stable throughout the four seasons, with an average of 0.95 for both measures (1 is the maximum score; Table 2). Almost all possible connections occurred, meaning that almost all pigs interacted with each other and did so reciprocally, as shown in Fig. 2. Across the seasons, a similar level of connections occurred: 86 connections out of 90 possible connections occurred in autumn; 84 out of 90 in winter; 70 out of 72 in spring and 68 out of 72 in summer. In- and out-degree centralization values (Table 2) indicate that both the initiation and receipt of affiliative interactions among the ten pigs were weakly centralized. The weak centralization indicates that interactions were distributed reasonably homogeneously across the group members.

Table 2
Values of density, reciprocity, and mean values of in-degree and out-degree centralization in the group of ten sows in each season.

	Autumn	Winter	Spring	Summer
Density	0.96	0.93	0.97	0.94
Arc reciprocity	0.95	0.93	0.97	0.94
Out-degree centralization	0.33	0.23	0.29	0.24
In-degree centralization	0.17	0.23	0.16	0.21

3.2. Preferential associations

The Monte Carlo test revealed the presence of preferential associations in each season, as the associations were not random. Out of the total number of connections that pigs formed, on average across the four seasons, 5.8 % consisted of strong associations, 35.7 % of weak associations and 58.5 % of no preferential associations. Autumn and winter had the highest percentage of strong associations (Table 3).

We then evaluated the repetition of preferential associations across the seasons. The Quadratic Assignment Procedure highlighted only a modest positive correlation between autumn and winter and no correlation between spring, summer and any of the other seasons (Table 4). No strong associations and only two weak associations were repeated across all four seasons. However, when analyzing autumn-winter, winter-spring and spring-summer separately, we observed that two strong and three weak associations remained stable between autumn and winter, only four weak associations repeated between winter and spring and seven weak associations repeated between spring and summer.

4. Discussion

In this study, we observed that pigs formed social preferences in each season, although from the possible interactions, approximately two-thirds were random, one-third-weak and around 6 % were strong preferences. However, it appears that these social preferences are not enduring over time, as indicated by a moderate correlation between the four seasons.

We calculated group density and reciprocity based on presumably affiliative behaviors such as gentle snout-body contact, snout-head contact, and allogrooming. The aim here was to assess the group cohesion and stability over a relatively extended period of time. A consistently high value over time of density and reciprocity, and a weak level of group centralization, demonstrates that the group of pigs exhibited a high level of cohesion and homogeneity throughout the four seasons. As the pigs had a large space allowance, and thereby the freedom to choose whether or not to interact, their high level of cohesion appears meaningful rather than random, as further confirmed by subsequent analyses of their social preferences. In the natural environment, wild boars tend to cluster with related individuals in spite of having the opportunity to disperse (Podgórski et al., 2014). We previously showed that this cohesion in domestic pigs is unrelated to thermal regulation (Seddaiu et al., 2024). It may be due to a need for being surrounded by familiar individuals as a result of predation risk creating benefits from being in a group and the inclusive fitness benefits of helping kin to survive rather than unrelated animals. It could also be due to a desire to maintain a threshold level of interaction, necessary to maintain familiarity (Fraser, 1974) and dominance relationships (Ewbank and Meese, 1971). To support this, contrary to what was observed in the case of social preferences, the removal and return of sows for farrowing between winter and spring, which can be seen as a potential social disruption, did not appear to significantly affect the measures of affiliation at the group level. Therefore, a reciprocity tending towards 1 across all four seasons would still demonstrate the need for a threshold level of affiliative interactions, as discussed above.

The distribution of weak and strong social preferences in this study

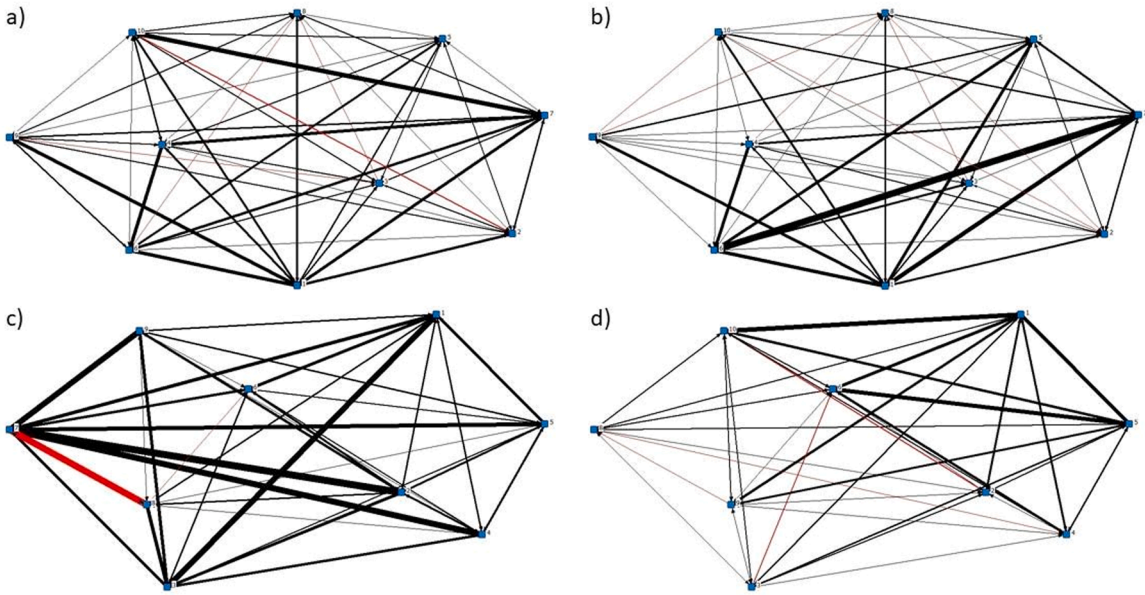

Fig. 2. Graphical representation of the social network of ten sows for autumn (a), winter (b), spring (c), and summer (d). Blue squares represent nodes, which correspond to the pigs, while the lines connecting the nodes represent interactions between them. The thicker the lines, the higher the frequency of contacts between the respective nodes. Black lines represent reciprocal contact, while red lines indicate unidirectional contact.

Table 3
Percentages of strong, weak or no associations for the group of 10 sows in each season.

	Autumn	Winter	Spring	Summer
Strong associations	8.9 %	8.9 %	2.8 %	2.8 %
Weak associations	31.1 %	31.1 %	41.7 %	38.9 %
No associations	60 %	60 %	55.6 %	58.3 %

Table 4
Pearson correlation coefficients between half-weight association index (HWI) matrices in the four seasons, * $p < 0.05$.

	Autumn	Winter	Spring
Winter	0.41*		
Spring	−0.0004	0.14	
Summer	0.12	0.21	−0.16

are consistent with previous studies examining interactions over a shorter period time (Goumon et al., 2020; Camerlink et al., 2023) and demonstrate that pigs in farm circumstances are capable of forming preferential associations. As these associations were based on direct engagement in social behaviours, they probably reflect true preferences. Other measures of association (e.g., proximity when resting or feeding) are harder to interpret as they may also be driven by non-social factors such as shared environmental preferences or diurnal patterns. Our results are also similar to what occurs in nature, where wild boars formed non-random associations, thus likely preferential, in 20–34 % of cases (Podgórski et al., 2014). The overall percentage of preferential associations remained consistent between autumn and winter; however, a notably lower number of strong preferences were observed during spring and summer. This alteration is likely attributable to the disruption to group cohesion caused by the removal of certain individuals for farrowing. The separation of pregnant sows prior to parturition is a standard practice in commercial farming. This is also what occurs in nature, where sows isolate themselves from the group for 1–2 weeks for farrowing. Perhaps the results we have found might indicate that this natural separation may also cause some disruption to preferential relationships, however the separation in nature is much shorter than occurs on a farm. A modest positive correlation between autumn and winter highlights that social preferences did not persist long, suggesting the absence of enduring social bonds.

4.1. Study limitations

The present study provides valuable insights into the social preferences of pigs over a prolonged period of time, yet certain limitations should be acknowledged. First, a small sample size (only 10 pigs) and one study group limits generalizability and reliability of results. However, a small sample size, combined with an extensive observation period (396 hour) ensured a level of detailed analysis of social interactions that is rarely achieved in studies with larger sample sizes. Moreover, farms that provide a large space allowance typically have only a small number of comparable groups, making it difficult to conduct large-scale studies under similar conditions. Additionally, the use of permutations strengthened the statistical robustness of the findings, ensuring that the observed social preferences were not merely random occurrences but reflected meaningful interactions between individuals.

In addition to the sample size, the homogeneity of the study population is another important consideration. Since seven of the pigs were from the same litter, it is possible that genetic and early environmental factors contributed to more uniform social behaviors within the group, which may not be reflective of the broader population in commercial farm settings. The findings observed in this experimental setting may, therefore, not be directly applicable to pigs reared under more variable or commercial conditions. This study's detailed analysis of a single but cohesive group can provide insights into social structures that may be valuable in environments where group sizes are constrained.

Lastly, while this study offers valuable data on the social structure and preferences of female pigs, the practical implications for pig welfare and management could be explored further. Although this study serves as an important first step, it is essential to emphasize that broader conclusions about the social relationships of pigs in commercial or welfare-driven contexts should be drawn with caution until further studies, with larger and more diverse sample sizes, are conducted.

5. Conclusion

Observations of affiliative behaviours across four seasons showed that pigs form social preferences. However, preferences were mostly weak and did not endure over time. The disruption to group cohesion, resulting from the removal of specific individuals for farrowing may have played a significant role in weakening social relationships among pigs. Despite the removal and return of sows, the herd maintained a cohesive and stable social structure across four seasons. In the majority of dyads, affiliative behaviours were reciprocated between individuals. Furthermore, the network density was high, indicating that almost every possible dyad showed affiliative interactions. The high density and reciprocity indicate that these behaviours are common and potentially of large importance to the social lives of these animals.

Ethics approval

Not applicable.

Declaration of generative AI and AI-assisted technologies

The authors did not use any artificial intelligence assisted technologies in the writing process.

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CRediT authorship contribution statement

Piero Seddaiu: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Simon P. Turner:** Writing – review & editing, Supervision, Methodology. **Irene Camerlink:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data are available online under CC BY 4.0 license at DOI: 10.17632/dcw686yc7z.1

References

Borgatti, S.P., Everett, M.G., Freeman, L.C., 2002. Ucinet 6 For Windows: Software for Social Network Analysis. Analytic Technologies, Harvard, MA.
Bray, J., Gilby, I.C., 2020. Social relationships among adult male chimpanzees (Pan troglodytes schweinfurthii): variation in the strength and quality of social bonds. Behav. Ecol. Sociobiol. 74, 1–19.
Büttner, K., Czycholl, I., Mees, K., Krieter, J., 2020. Social network analysis in pigs: impacts of significant dyads on general network and centrality parameters. Animal 14 (2), 368–378.
Cairns, S.J., Schwager, S.J., 1987. A comparison of association indices. Anim Behav 35 (5), 1454–1469.
Camerlink, I., Scheck, K., Cadman, T., Rault, J.L., 2023. Effects of preferential social associations on pigs' response to weaning. animal 17 (6), 100846.
Durrell, J.L., Sneddon, I.A., O'connell, N.E., Whitehead, H., 2004. Do pigs form preferential associations? Appl. Animal Behav. Sci. 89 (1–2), 41–52.
Ewbank, R., Meese, G.B., 1971. Aggressive behavior in groups of domesticated pigs on removal and return of individuals. Animal Sci. 13 (4), 685–693.
Farine, D.R., Whitehead, H., 2015. Constructing, conducting and interpreting animal social network analysis. J. Animal Ecol. 84 (5), 1144–1163.
Fone, K.C., Porkess, M.V., 2008. Behavioral and neurochemical effects of post-weaning social isolation in rodents—Relevance to developmental neuropsychiatric disorders. Neurosci. Biobehav. Rev. 32 (6), 1087–1102.
Fraser, D., 1974. The behavior of growing pigs during experimental social encounters. J Agric Sci 82 (1), 147–163.
Gero, S., Bejder, L., Whitehead, H., Mann, J., Connor, R.C., 2005. Behaviorally specific preferred associations in bottlenose dolphins, Tursiops spp. Can. J. Zool. 83 (12), 1566–1573.
Ginsberg, J.R., Young, T.P., 1992. Measuring association between individuals or groups in behavioural studies. Anim Behav. 44 (1), 377–379.
Goumon, S., Illmann, G., Leszkowová, I., Dostalová, A., Cantor, M., 2020. Dyadic affiliate preferences in a stable group of domestic pigs. Appl. Animal Behav. Sci. 230, 105045.
Gutmann, A.K., Špinka, M., Winckler, C., 2015. Long-term familiarity creates preferred social partners in dairy cows. Appl. Animal Behav. Sci. 169, 1–8.
Hanneman, R.A., & Riddle, M. 2005. Introduction to social network methods.
Hinde, R.A., 1976. Interactions, relationships and social structure. Man 1–17.
Jowett, S.L., Barker, Z.E., Amory, J.R., 2023. Preferential associations in an unstable social network: applying social network analysis to a dynamic sow herd. Front. Veterin. Sci. 10, 1166632.
Lee, V.E., Arnott, G., Turner, S.P., 2022. Social behavior in farm animals: applying fundamental theory to improve animal welfare. Front. Veterin. Sci. 9, 932217.
Li, Y., Zhang, H., Johnston, L.J., Martin, W., 2018. Understanding tail-biting in pigs through social network analysis. Animals 8 (1), 13.
McLennan, K.M., 2013. Social Bonds in Dairy cattle: the Effect of Dynamic Group Systems On Welfare and Productivity. University of Northampton. Doctoral dissertation.
Meese, G.B., Ewbank, R., 1973. The establishment and nature of the dominance hierarchy in the domesticated pig. Anim Behav 21 (2), 326–334.
Muller, Z., Cantor, M., Cuthill, I.C., Harris, S., 2018. Giraffe social preferences are context dependent. Animal Behav. 146, 37–49.
Ozella, L., Price, E., Langford, J., Lewis, K.E., Cattuto, C., Croft, D.P., 2022. Association networks and social temporal dynamics in ewes and lambs. Appl. Animal Behav. Sci. 246, 105515.
Ozella, L., Giacobini, M., Diaz, E.V., Schiavone, A., Forte, C., 2023. A comparative study of social behavior in primiparous and multiparous dairy cows during automatic milking. Applied Animal Behav. Science 268, 106065.
Perryman, R.J., Venables, S.K., Tapilatu, R.F., Marshall, A.D., Brown, C., Franks, D.W., 2019. Social preferences and network structure in a population of reef manta rays. Behav. Ecol. Sociobiol. 73 (8), 1–18.
Podgórski, T., Lusseau, D., Scandura, M., Sönnichsen, L., Jędrzejewska, B., 2014. Long-lasting, kin-directed female interactions in a spatially structured wild boar social network. PLoS One 9 (6), e99875.
Prevolnik Povše, M., Mesarec, N., Skok, J., Škorjanc, D., 2021. Agonistic interactions between littermates reappear after mixing multiple litters at weaning in pigs. Agriculture 11 (9), 844.
Seddaiu, P., Turner, S.P., Camerlink, I., 2024. Cross-seasonal and diurnal variation in physical contact between sub-adult pigs. Appl. Animal Behav. Sci. 278, 106379.
Silk, J.B., Alberts, S.C., Altmann, J., 2003. Social bonds of female babies enhance infant survival. Science 302 (5648), 1231–1234.
Silk, J.B., Altmann, J., Alberts, S.C., 2006. Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61, 183–195.
Schülke, O., Wenzel, S., Ostner, J., 2013. Paternal relatedness predicts the strength of social bonds among female rhesus macaques. PLoS One 8 (3), e59789.
Weidt, A., Hofmann, S.E., König, B., 2008. Not only mate choice matters: fitness consequences of social partner choice in female house mice. Animal Behav. 75 (3), 801–808.
Wey, T., Blumstein, D.T., Shen, W., Jordan, F., 2008. Social network analysis of Animal Behav.: a promising tool for the study of sociality. Animal Behav. 75 (2), 333–344.

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Social behavioural profiles in pigs and the role of sex, dominance and kinship

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ABSTRACT

Affiliative behaviours in pigs can enhance group cohesion and lower stress levels, ultimately improving individual welfare. Individual factors such as dominance rank, sex or kinship may play a key role in shaping the expression of social behaviours, but there is a lack of knowledge on the contribution of these variables. The aim of this study was to identify social behavioural profiles in pigs, based on putative affiliative behaviours, and evaluate the extent to which dominance rank, sex, and kinship influence their expression. Agonistic interactions were recorded on 212 male and female domestic pigs (*Sus scrofa domesticus*) to calculate dominance ranks within 16 groups. Based on this, 96 pigs (six pigs per group) were selected for observations on detailed social nosing behaviours, allogrooming, spatial proximity and social play. Principal components analysis was used to assess the presence of behavioural profiles, followed by mixed model analysis to evaluate the influence of individual factors on each principal component (**PC**). Snout contact constituted the majority of interactions and was exhibited by all pigs. Lying in body contact and snout–snout proximity were also frequent and were expressed by more than 95% of individuals. Allogrooming and social play were observed in 29.2 and 33.3% of pigs, respectively, and represented less than 1% of the total interaction frequency. Three PCs had eigenvalues > 1 and together explained 60.9% of the variance. The PCs related to social contact (**PC1**), proximity (**PC2**) and social engagement (**PC3**). Sex, dominance status and kinship had no effect on PC1 or PC3, but sex and kinship had a limited effect on PC2, with entire males showing more snout proximity than females ($P < 0.001$) and pigs showing less snout proximity behaviours towards their kin ($P = 0.044$). This study shows that the expression of putatively affiliative social behaviours can be clustered into profiles and is under commercial settings only marginally influenced by individual factors such as dominance and kinship, suggesting their general relevance to pigs' social life.

Implications

This study examined physical contact and proximity behaviours in group-housed pigs. Pigs differed in their social behavioural profiles, expressing varying degrees of social contact, proximity, and social engagement. This suggests that social behaviour in pigs is flexible rather than fixed into discrete types. In commercial environments where pigs are housed in groups, recognising such individual variation may help explain differences in social dynamics and group cohesion. The observed sex difference in proximity behaviours further indicates that management strategies may need to consider sex-specific social tendencies. Overall, these findings highlight the importance of accounting for individual social variation in farmed pigs.

Introduction

Social behaviours are crucial to the development of animals, particularly in highly social species (Snyder-Mackler et al., 2020; Lee et al., 2022). Among these, affiliative behaviours — those that promote social bonding and cohesion — play a key role in maintaining group stability, reducing stress, and supporting individual welfare (Cameron et al., 2009; Silk et al., 2010; Campbell et al., 2018). In farm animals such as domestic pigs (*Sus scrofa*), these interactions have been linked to better welfare (Val-Laillet et al., 2009; Rault, 2019). Affiliative behaviours are also commonly shown in wild animals, where they may play an important role in maintaining social bonds that are adaptive and benefit fitness (Silk et al., 2010; Snyder-Mackler et al., 2020). Despite the importance of affiliative behaviour, it has received much less research interest in farm animals than agonistic or competitive behaviour (Boissy et al., 2007; Rault, 2012). Understanding the dynamics of

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affiliative behaviours in farm animals is therefore of fundamental importance, especially in the context of animal husbandry, where group composition is often manipulated.

In pigs, affiliative behaviours have been described in a variety of contexts, including postconflict affiliation (Cordoni et al. 2023), social cohesion (Camerlink et al., 2014), and stress buffering (Reimert et al., 2014; Khatiwada et al., 2025a). Several behaviours may be considered as putatively affiliative due to their occurrence across various contexts, including agonistic events, indicating that these behaviours may not always be purely affiliative, and their function can depend on the social context (Goumon et al., 2025). Such behaviours include allogrooming (Meynhardt, 1982; Seddaiu et al., 2025), resting in body contact (Newberry and Swanson, 2001; Seddaiu et al., 2024), social play (Horback, 2014; Brown et al., 2015; Steinerová et al., 2024) and snout contact (Camerlink and Turner 2013; Khatiwada et al., 2025b). The nature and frequency of the aforementioned behaviours, as well as the factors that influence them, are still under investigation.

Recent studies have shown that behaviours such as snout contact and lying in body contact can depend on external conditions such as ambient temperature (Camerlink et al., 2022a) and group stability (Khatiwada et al., 2025b). However, the influence of individual factors on the expression of affiliative interaction, such as sex, genetic relatedness and dominance status, is not yet clear. Two studies on groups of growing pigs reported that sex, dominance status and genetic relatedness were only partially related to potentially affiliative behaviours (Goumon et al., 2020; Clouard et al., 2024). However, other studies have shown that there is an effect of dominance status on spatial proximity in pigs, with dominant pigs often spacing further away from others, eventually resulting in less social interactions initiated (McCort and Graves, 1982). Moreover, a sex effect has been seen in conflict avoidance behaviours, where entire males often engaged in ritualised interactions (i.e. proximity-based interactions) before escalating into fights, whereas females attacked sooner (Camerlink et al., 2022b). Sex differences have also been reported in social nosing interactions among piglets (Clouard et al., 2022). Further, familiarity might influence the expression of a range of social behaviours, with familiar pigs nearly twice as likely to express snout contact (Jowett et al., 2025). Despite growing interest in affiliative behaviours in farm animals (Goumon et al., 2025), there is a limited and contradictory understanding of how these individual factors interact to shape their expression.

The aim of this study was to identify behavioural profiles in pigs based on putatively affiliative behaviours and evaluate the extent to which dominance rank, sex, and kinship influence their expression. While most recent studies on pig sociality have focused on single behaviours, these provide only a partial view of the complexity of social life. In contrast, this study takes a wider lens, analysing how behaviours can co-occur to form distinct behavioural profiles. Based on the existing literature, we hypothesised that genetically related individuals would show more social interactions, that males would display more frequent proximity-related behaviours than females, and that dominant individuals would initiate fewer social interactions than mid– or low–ranked individuals, after accounting for the effect of sex.

Material and methods

Animals and housing

In total, 16 groups of domestic pigs (Large White × Landrace sows × American Hampshire boars) were studied in the Easter Howgate Pig Research Unit from August 2024 to March 2025. A total of 212 pigs (n = 108 entire males and n = 104 females) from three farrowing batches were observed for dominance rank. Each batch was observed in a different month. From these, 96 pigs (47 males and 49 females) were further observed as focal animals (described below). Cross-fostering was kept to a minimum and done only for litters with more than 10 piglets and where the sow had a body condition below the herd average. Pigs were weaned at 4 weeks and regrouped into single-sex groups. At 8 weeks of age, pigs were regrouped into new single sex groups of 10–16 individuals each. While mixing events are known to influence social behaviour in pigs (Petherick and Blackshaw, 1987), all individuals experienced the same mixing history, allowing behavioural variation to be examined under comparable social conditions. The study started after this second event of mixing at 8 weeks of age and finished at 12 weeks of age. Pigs were grouped by similar weight and siblings were divided over as many pens as possible, whilst ensuring that each pig had at least one sibling and one pig from the same weaning pen in their new group. Female pigs were housed in pens that previously housed males and vice versa, so that no pig remained in its original pen, to avoid the effect of home pen territory on aggression. The groups were housed in enriched conditions with a floor space of 6.9 × 2.1 m (14.49 m^2; 1.45–0.91 m^2/pig). Straw was provided as bedding material, with dirty straw removed and fresh straw added as necessary each day. One Porcichew toy (Ketchum manufacturing company, UK) and one length of Manila rope (Westward Rope and Wire, UK) hung from the pen wall were provided as enrichment objects. Shed temperature was adjusted according to the age of pigs and controlled automatically. Food and water were provided *ad libitum*. Pigs were individually recognised by their ear tag and by a spray mark applied on their back with animal marker spray (East Riding Farm Services, UK). The back mark for identification was redone twice a week, in the morning, at least 1 h before starting the observations. Daily checks were done to evaluate the pigs' health.

Dominance rank analysis

For the first week of observations, after regrouping at week 8, only agonistic behaviours were scored with the aim to calculate dominance relationships. In particular, submissive behaviour was scored to assess who lost the encounter. Submissive behaviour was scored as withdrawal during an agonistic encounter, including a head-tilt-retreat, whereby the losing pig lowers its head and turns it rapidly sideways (Jensen, 1980), thereby turning the shoulder away from the opponent and refraining from retaliation for at least 10 s (Camerlink et al., 2016). Agonistic interactions where it was unclear whether a head-tilt-retreat had occurred were recorded as inconclusive. Pigs were observed by continuous observations for a total of 5 h per pen through live and video recordings between 0900 and 1600 h. Subsequently, a dominance score was determined for each individual using the Glicko rating from the agonistic interactions with a clear outcome. Glicko rating is a system for establishing which individual is dominant based on the outcomes of their fights. The system assigns a greater increase in score to an individual when it defeats a highly successful individual than a less successful individual. It incorporates a rating value and a rating deviation (**RD**), which quantifies the certainty of the rating (Glickman, 1999). The model is particularly well-suited for datasets with varying numbers of interactions per individual and allowed us to determine a dominance rank from the individual scores. Glicko ratings were calculated in R software version 4.5.1 (R Core Team, 2025), using the "PlayerRatings" package (Stephenson and Sonas, 2012). After the analysis, each pig had a final rating value and a final RD based firstly on the number of victories and defeats, and also on the relative dominance exhibited during each interaction. The final ranking was determined by both the rating value and the associated RD, reflecting not only perfor-

mance outcomes but also the confidence in those estimates. Default values were set at 2 200 for the rating and 300 for the RD.

Behavioural observations

Based on the Glicko ratings, six focal pigs were selected per group. For each group, two pigs with the highest, the middle and the lowest ranks based on their Glicko scores were selected for further observations. The RD was not used in the selection of focal pigs. This resulted in 96 pigs (males and females) being included in the study. Observing six focal pigs instead of 10–16 allowed for more manageable and thus more detailed observations, leading to more accurate and reliable results. Additionally, by selecting from across the dominance hierarchy, a balanced representation within each group was maintained. The focal animals were observed in weeks 10 and 11 using the ethogram described in Table 1, using continuous observations. All interactions were scored as single events and attributed to one actor, meaning that in the case of repeated events in a short time, every contact was scored. For each interaction, the actor was defined as the individual who initiated the behaviour, regardless of whether the recipient was a focal or non-focal pig. Interactions between two focal pigs were recorded once, attributed only to the initiating individual. In case of behaviours that could appear symmetrical, the actor was identified as the pig that initiated the approach leading to the interaction. If no clear initiator could be identified, the interaction was not scored. Pigs were observed for 10 days over 2 weeks, 5 days a week, for a total of 10 h of continuous observation per pen, resulting in 160 h in total. All observations were performed using the Animal Behaviour Pro App, version 1.2 (University of Kent, Canterbury, UK), installed on an iPad.

Statistical analysis

For each pig, we analysed the total frequency of initiated interactions for each behaviour and based on that constructed a frequency matrix in Excel. The descriptive statistics were conducted in Excel 2019 and the Principal Component Analysis (**PCA**) and mixed models in R version 4.5.1. As descriptive analysis, for each behavioural variable, we calculated the total number of occurrences, the average frequency per individual, the percentage of individuals expressing the behaviour at least once, and the percentage of each behaviour expression relative to the total (Table 2).

Principal component analysis

The first aim of our analysis was to identify behavioural profiles in our sample with PCA. This approach reduces data dimensionality by transforming the original variables into a new set of uncorrelated variables (principal components, **PCs**) that capture most of the dataset's variance (Abdi and Williams, 2010). Each PC is characterised by a set of co-occurring behaviours and can therefore be interpreted as a behavioural profile. Individual PC scores reflect the extent to which each animal expressed that profile. All behavioural variables were available for all focal individuals. Zero values reflected the absence of a behaviour during the observation period rather than missing observations; therefore, no data removal or imputation was required prior to the PCA. Before extracting the principal components, the data were standardised (argument scale = TRUE in the prcomp function) using z-transformation (mean = 0, SD = 1) and inspected for outliers using boxplots, with observations identified as outliers if they had a z-value greater than 3, following Tabachnick et al. (2007). A small number of outliers were identified (12 data points out of 864 behavioural measurements across 11 individuals); however, sensitivity analyses excluding these individuals produced a comparable PCA structure. Results from the full dataset were therefore considered. We then assessed the suitability of the dataset for PCA analysis. Pearson correlations were calculated between all z-transformed variables. The Kaiser-Meyer-Olkin measure of sampling adequacy was 0.73, and Bartlett's test of sphericity was significant (χ^2 = 171.86, P < 0.001), indicating that the correlation structure of the behavioural variables was suitable for PCA. We performed a PCA with orthogonal rotation using the prcomp function from "stats" package to run the analysis. We used the "factoextra" package (Kassambara and Mundt, 2016) to visualise the results with graphs. Once all principal components were extracted, only those with eigenvalues exceeding 1 were retained for further analysis, following the Kaiser criterion (Kaiser, 1960).

Mixed models

Once the principal components were identified, we aimed to assess the influence of dominance rank, sex, and kinship on the expression of each component. To do so, we extracted the PC scores for each individual across all three components. These scores were then used as response variables in linear mixed models, using the lmer function from the "lme4" package in R (Bates et al., 2024). Sex (male vs. female), dominance score (high, mid, low), and kinship-based interactions (proportion) were included as fixed effects. Variables pen and batch, which also accounted for seasonal fluctuations, were added as random effects. Model assumptions were assessed by inspecting the residuals. Histograms and QQ-plots indicated approximate normality, and residuals versus fitted values plots confirmed homoscedasticity. Multicollinearity among fixed effects was evaluated using variance inflation factors (**VIFs**), with all VIFs well below 5 (dominance: 1.00, kinship-based interactions: 1.01, sex: 1.00), indicating no collinearity among fixed

Table 1
Ethogram for observed behaviours in 96 growing pigs of 10–11 weeks of age.

Behaviour	Description
Snout-snout contact	Touches another pig's snout with its nose disc; includes the nose disc of the recipient
Snout-snout proximity	A pig extends its snout in direction of the snout of another pig snout at approximately <30 cm distance without making contact
Snout-head contact	Touches another pig's head with its nose disc; excludes the snout and allogrooming
Snout-head proximity	A pig extends its snout in the direction of the head of another pig at <30 cm distance without making contact; excludes snout
Snout-body contact	Touches the body of another pig with its nose disc, excluding the head
Allogrooming	Gently nibbles or licks the body or head of another pig; does not cause acute skin damage to the other pig
Lying in body contact head-to-head	Focal pig actively lies down with its body in contact with a conspecific in a parallel orientation with their heads adjacent to or touching
Lying in body contact any other orientation	Focal pig actively lies down with its body in contact with a conspecific in a parallel head-to-tail, or non-parallel orientation
Social play	A playful interaction characterised by one or more of the following behaviours: running (incl. chasing), hopping, flopping, tossing, pushing or nudging without delivering or receiving potentially damaging aggression. It involves at least one other individual besides the actor.

Table 2
Frequency distribution of observed social behaviours. Columns show total occurrences across all animals, average frequency per pig, percentage of pigs expressing the behaviour, and percentage of each behaviour expression relative to total. A total of 7 097 interactions were scored during 160 h of observations from 96 pigs (16 groups) aged 10–11 weeks.

Behaviour	Total occurrences	Average frequency per pig	% of pigs performing behaviour	% of total interactions
Snout-body contact	1 925	20.1	100%	27.1%
Snout-snout contact	1 628	17.0	100%	22.9%
Snout-head contact	1 186	12.4	100%	16.7%
Lying in body contact any other orientation	775	8.1	99.0%	10.9%
Lying in body contact head-to-head	634	6.6	97.9%	8.9%
Snout-snout proximity	602	6.3	96.9%	8.5%
Snout-head proximity	253	2.6	85.4%	3.6%
Allogrooming	44	0.5	29.2%	0.6%
Social play	50	0.5	33.3%	0.7%

effects. *P*-values < 0.05 were considered significant. For the kinship-based interactions, because the number of siblings varied between groups, as well as the total number of group members, we corrected kin interaction rates according to the opportunity pigs had of interacting with a sibling. For each focal pig and behaviour, we calculated an adjusted kinship proportion, defined as:

$$\textit{Adjusted kinship proportion} = \frac{N\ \textit{interactions with kin}/N\ \textit{total interactions}}{N\ \textit{siblings in a group}/N\ \textit{individuals in a group} - 1}$$

This formula calculates whether individuals interacted with kin more or less than expected based on availability and is derived from the simple ratio index from Whitehead and James (2015). Values > 1 indicate a bias towards kin, values = 1 indicate interactions proportional to availability, and values < 1 indicate kin avoidance.

Results

Dominance ranks and behavioural expression

Glicko rating values, reflecting dominance ranks, ranged from 1 433 to 2 970 across all 212 individuals (2 189 ± 314.8 SD). The rating deviation, which quantifies the certainty of the rating, ranged from 106.1 to 237.2 (149.8 ± 22.88 SD). Pigs who consistently won encounters exhibited higher ratings and lower RD values. In contrast, individuals with fewer interactions or inconsistent win-loss outcomes had higher RD values, reflecting increased uncertainty. Before conducting the PCA, we examined the frequency of each behaviour (Table 2). The majority of interactions consisted of nosing contacts. Behaviours such as lying in body contact and snout–snout proximity were also common and were expressed by more than 95% of individuals. In contrast, low-frequency behaviours such as allogrooming and social play were observed in 29.2 and 33.3% of pigs, respectively. Although these behaviours occurred less frequently overall (< 1% of total interactions), they still contributed to individual variation and were therefore retained in the PCA.

Behavioural profiles

The PCA on the social behaviours of 96 focal pigs identified nine components with distinct loading profiles. However, only three principal components (**PC1**, **PC2**, and **PC3**) had eigenvalues greater than 1 and were therefore selected for further analysis. These three components combined explained a total of 60.9% of the variance among the behavioural variables (Table 3). PC1 presented strong positive loadings (≥0.5) on the frequency of making snout contact with the snout or the head of another pig, as well as on lying in body contact with a conspecific (head-to-head or in any other orientation). Behaviours belonging to PC1 were the most frequent, constituting a minimum of 8.9% and a maximum of 27.1% of the total recorded frequencies. Furthermore, almost all the individuals expressed these behaviours (97%–100%) (Table 2). PC2 showed high positive loadings on proximity behaviours (snout-to-snout and snout-to-head). These behaviours accounted for 8.5 and 3.6% of all behavioural occurrences and were expressed by 96.9 and 85.4% of individuals (Table 2). Consequently, they were less common than the behaviours that loaded most strongly onto PC1. PC3 exhibited high positive loadings on allogrooming and social play. PC3 behaviours occurred much less frequently (allogrooming: 0.6% and social play: 0.7%) and were expressed by only 29.2 and 33.3% of individuals (Table 2). Based on these behavioural associations, the components were labelled as follows: PC1 - social contact, PC2 - proximity, and PC3 - social engagement.

Table 3
Principal component analysis (PCA) loading scores of behaviour measurements on principal component 1 (PC1), principal component 2 (PC2) and principal component 3 (PC3). Based on social interactions observed in 96 pigs (16 groups) of 10–11 weeks of age.

Behaviour	PC1	PC2	PC3
Snout-snout contact	0.782	−0.018	0.168
Snout-snout proximity	0.059	0.851	0.080
Snout-head contact	0.815	0.104	0.096
Snout-head proximity	0.135	0.808	−0.061
Snout-body contact	0.566	0.188	0.068
Allogrooming	0.023	0.095	0.904
Lying in body contact head-to-head	0.688	−0.038	0.096
Lying in body contact any other orientation	0.742	−0.021	−0.152
Social play	0.228	−0.441	0.503
Variance explained	31%	18.2%	11.7%
Eigenvalue	2.791	1.636	1.053

The role of sex, dominance rank and kinship

In the mixed model analysis, sex, dominance rank and kinship did not significantly influence PC1 'social contact' or PC3 'social engagement' (Fig. 1). However, sex influenced PC2 'proximity' (estimate: 1.17 ± 0.16 SE, $P < 0.001$), indicating that males engaged more frequently in the proximity behaviours with higher loadings on this component than females (Fig. 2). Kinship had a limited effect on PC2 scores (estimate: −0.36 ± 0.18 SE, $P = 0.044$), indicating that higher relatedness was associated with lower PC2 values.

Discussion

This study explored how domestic pigs form behavioural profiles based on putatively affiliative behaviours and to what extent the behavioural profiles are shaped by individual factors. We expected that individuals would exhibit behavioural profiles, each characterised by different combinations of behaviours. Principal

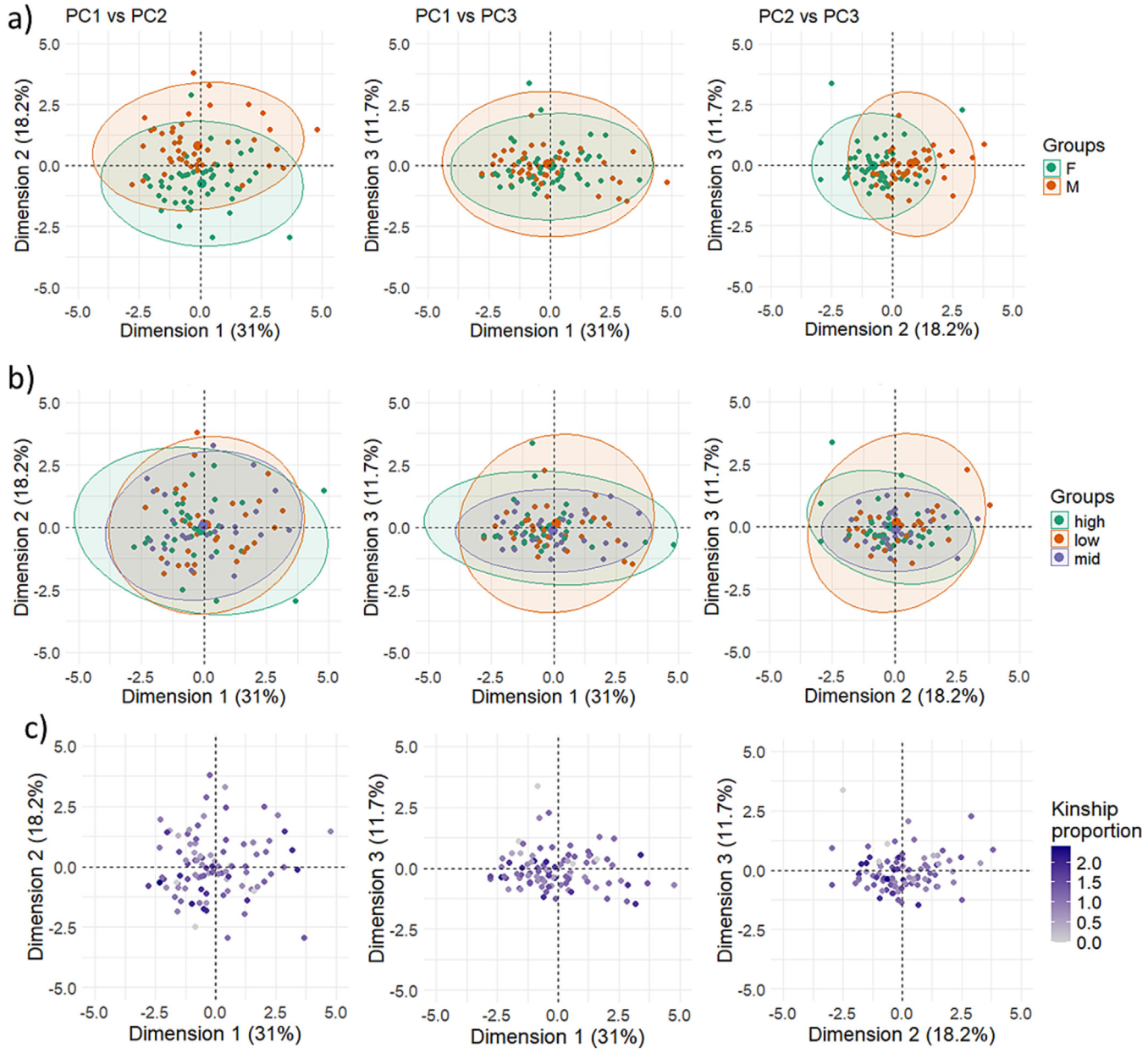

Fig. 1. Principal Component Analysis (PCA) scatterplots showing the distribution of individual pigs along the first three principal components. Each plot shows a combination of the first three principal components (PCs), with PCs and their variance on x- or y-axis. Each point represents one individual (n = 96 pigs). (a) PCA score plots grouped by sex (female (F), male (M)) with 95% confidence ellipses. (b) PCA score plots grouped by dominance status (high, mid, low), with 95% confidence ellipses. (c) PCA score plots coloured by kinship proportion within the social group, where darker shades indicate a higher proportion of kin interactions.

Components were interpreted to represent 'social contact', 'proximity' and 'social engagement' and together explained 60.9% of the variation. We hypothesised that subordinate pigs would initiate fewer social interactions, for which we found no evidence. However, the hypothesis that males would display more frequent proximity-related behaviours than females was indeed confirmed, based on PC2. Against expectation, kinship did have a limited effect on social tendencies.

From the PCA, three clear PCs were extracted. PC1 (social contact) was characterised by high loadings of behaviours involving direct physical contact, such as snout contact and lying in body contact. PC1 explained the greatest percentage of variance among all components (31%) and included the most frequent behaviours. Snout contact and lying in contact have been frequently used in studies on affiliative behaviour in pigs (Goumon et al., 2025), but most studies so far suggest that these two behaviours are distinctly different and may represent separate facets (Camerlink et al., 2022a; Clouard et al., 2024). Snout contact serves various social functions, including affiliative contact, whereas lying in body contact has, in recent studies, been shown to be less strongly associated with the maintenance of affiliative relationships (Goumon et al., 2025). Snout contact and lying in contact may occur as part of short behavioural sequences, such as social nosing before approaching a lying recipient (Camerlink and Turner, 2013). This interpretation also helps explain the covariation highlighted by the PCA. As an exploratory and descriptive method, PCA identifies patterns of behavioural co-occurrence and does not imply a biological function. Nevertheless, because these behaviours were the most frequently expressed and involved nearly all individuals, they may

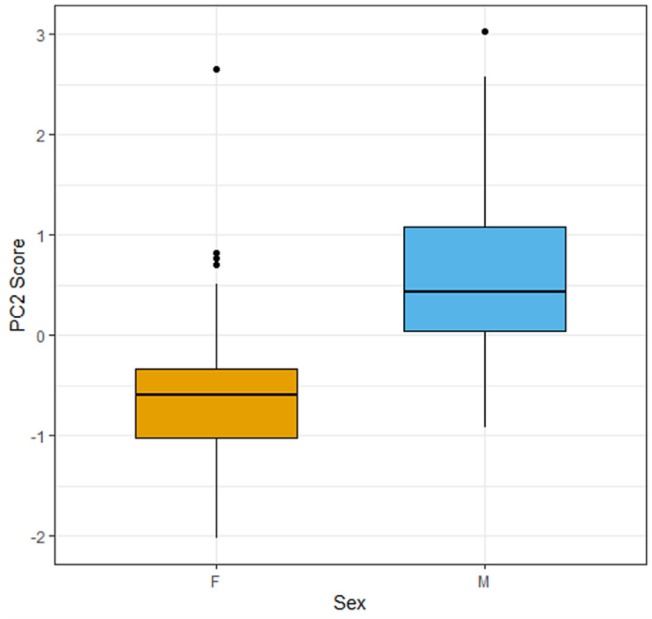

Fig. 2. (a) Boxplot of the distribution of principal component 2 (PC2) scores (y-axis) for female (F) and male (M) pigs (x-axis). The boxes represent the interquartile range (IQR), which contains the middle 50% of the data. The horizontal line inside the boxes represents the median. The vertical lines extending from the box (whiskers) reach the minimum and maximum values, excluding outliers.

have a central role in the social behaviour of pigs. Moreover, the use of interaction frequency rather than duration makes the two contact behaviours seem more similar (being both the most frequently expressed and involving nearly all individuals). In the present study, frequency-based measures were considered more appropriate than duration-based measures to address the objective, as they more directly reflect individual decisions to initiate social interactions. The mixed model analysis showed that dominance rank, sex, and kinship did not significantly influence PC1 scores, indicating that variation in social contact behaviours was not strongly related to these factors. It may indicate that physical contact is of general relevance to social life in pigs (Seddaiu et al., 2024), and it is not strictly related to individual factors.

PC2 (proximity) was characterised by high loadings of snout proximity and explained 18% of the variance among all components. The finding that 'snout contact' (PC1) and 'proximity' (PC2) emerged as separate components is in line with recent literature that shows that these two similar behaviours (snout contact and snout proximity) have a subtle but distinct meaning for pigs (Khatiwada et al., 2025b; Jowett et al., 2025). Snout proximity has previously been associated with social recognition (Kristensen et al., 2001), which may switch to conflict avoidance and risk aversion during social instability (Khatiwada et al., 2025b). The distinction between snout proximity and snout contact even extends to an inverse relationship with growth, where snout contact relates to BW gain and snout proximity to weight loss (Khatiwada et al., 2025b). Males had a substantially higher score on this PC than females, showing that they are involved in more proximity-related behaviours. Prepubertal entire males were observed to show more proximity-related behaviours than females during agonistic interactions (Camerlink et al., 2022b), which was related to conflict avoidance behaviour. The snout proximity during such ritualised agonistic interactions has greater risks involved than during regular interactions (Camerlink et al., 2022b) and may facilitate conflict avoidance by allowing social assessment without direct physical contact (Khatiwada et al., 2025b). In addition, pigs showed less snout proximity towards their kin, consistent with the idea that snout proximity might serve as recognition and information gathering, while limiting potentially risky interactions with close kin. The effect of sex and kinship on proximity-related behaviours highlights subtle differences in individual sociality that may help refine management practices aimed at improving welfare. For example, increased space allowance (Chidgey, 2024) and barriers to hide behind (McGlone and Curtis, 1985; Bulens et al., 2017) could facilitate the expression of proximity behaviours. While these strategies may be particularly beneficial to entire males, they may also benefit females, accommodating individual variation across pigs. From an evolutionary perspective, these behavioural profiles may reflect pigs' social competence and behavioural flexibility, which play a key role in adaptation (Taborsky and Oliveira, 2012; Kappeler et al., 2019).

PC3, labelled as social engagement, explained 11.9% of the total variance. It was uniquely composed by allogrooming and social play. Social play in juveniles or adults and allogrooming are infrequently occurring behaviours, which were shown in this study as well as in previous studies (social play: Newberry et al., 1988; Zupan et al., 2019; allogrooming: Seddaiu et al., 2024). Aside from their infrequent occurrence, there are strong individual differences in their expression (play: Brown et al., 2015), with some pigs rarely showing these behaviours, whereas others perform them more frequently (Seddaiu et al., 2024). We did not find an effect of individual factors on PC3. This was unexpected as previous literature indicates that play is shown more by males (Brown et al., 2015; Weller et al., 2019). The reason for this absence might be the combination of allogrooming and social play in the same component. In addition, both Brown et al. (2015) and Weller et al. (2019) studied mixed-sex groups (preweaning stage), whereas in the present study, pigs were housed in single-sex groups. This housing condition might have reduced sex differences in social play frequency. Moreover, social play in pigs is generally inclusive, allowing multiple group members to join (Horback, 2014). This suggests that pigs who initiate social play or give play invites are more socially engaged, independently of internal factors. Furthermore, while allogrooming would be assumed to occur between closely related individuals or those with a high degree of familiarity, there is so far no evidence for this (Clouard et al., 2024).

The dominance status of each individual was assessed through Glicko rating, with higher ratings reflecting more consistent success in agonistic encounters and an ability to defeat other successful animals. The Glicko rating provided a useful method to reflect more precisely the agonistic interactions within the group, while taking into account the opponent's prior wins and defeats (Glickman, 1999). Domestic pigs establish a relatively stable social hierarchy (through dominance relationships) (Meese and Ewbank, 1973), which is partly based on strength as a result of BW (Lanthony et al., 2022). The Glicko rating did provide a linear hierarchy structure from which we selected the top, mid– and bottom –ranked animals. Nevertheless, their dominance rank did not influence any of the PCs for behaviour, which is in contrast with former studies showing that dominant pigs space further away and may initiate fewer social interactions (McCort and Graves, 1982). Although dominance hierarchies in pigs are typically established within approximately the first 24 h after mixing (Meese and Ewbank, 1973), aggression can continue in the long term due to competition for space and access to resources (Tan et al., 1991). As groups were regrouped only 2 weeks prior, it may be that the hierarchy was still unstable, resulting in a lack of effect of dominance on the PCs. Another explanation is that resources were abundant, reducing the need to enforce dominance hierarchies. It may also be that these social behaviours are expressed regardless of social rank.

Conclusions

Observations of putative affiliative behaviours on 96 domestic pigs highlighted the presence of three affiliative behavioural profiles: social contact, proximity and social engagement. The profiles were partially influenced by individual characteristics of dominance rank, sex and the relative frequency of kinship-based interactions. The study highlights the difference between behaviours of direct physical contact and those performed in close social proximity without making contact. Together, the results emphasise the social complexity of pigs' behaviour repertoire, especially for nuanced micro-behaviours related to affiliative interactions.

Ethics approval

The study was part of a larger overarching research project on social competence in pigs. The study protocol was approved by SRUC's Animal Experiments Committee. This non-invasive behavioural study was part of a larger experiment authorised by the UK Home Office (Project licence P3850A80D/PP1403242).

Data and model availability statement

Data are available online under CC BY 4.0 licence at https://doi.org/10.17632/r2svdf6zyh.1. 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 author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Abdi, H., Williams, L.J., 2010. Principal component analysis. Wiley Interdisciplinary Reviews: Computational Statistics 2, 433–459.
Bates, D. et al., 2024. lme4: linear mixed-effects models using 'Eigen'and S4. Retrieved on 12 October 2025 from: https://cran.rproject.org/web/packages/lme4/index.html.
Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., Keeling, L.J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., Aubert, A., 2007. Assessment of positive emotions in animals to improve their welfare. Physiology & Behavior 92, 375–397.
Brown, S.M., Klaffenböck, M., Nevison, I.M., Lawrence, A.B., 2015. Evidence for litter differences in play behaviour in pre-weaned pigs. Applied Animal Behaviour Science 172, 17–25.
Bulens, A., Van Beirendonck, S., Van Thielen, J., Buys, N., Driessen, B., 2017. Hiding walls for fattening pigs: do they affect behavior and performance? Applied Animal Behaviour Science 195, 32–37.
Camerlink, I., Turner, S.P., 2013. The pig's nose and its role in dominance relationships and harmful behaviour. Applied Animal Behaviour Science 145, 84–91.
Camerlink, I., Arnott, G., Farish, M., Turner, S.P., 2016. Complex contests and the influence of aggressiveness in pigs. Animal Behaviour 121, 71–78.
Camerlink, I., Scheck, K., Cadman, T., Rault, J.L., 2022a. Lying in spatial proximity and active social behaviours capture different information when analysed at group level in indoor-housed pigs. Applied Animal Behaviour Science 246, 105540.
Camerlink, I., Farish, M., Arnott, G., Turner, S.P., 2022b. Sexual dimorphism in ritualized agonistic behaviour, fighting ability and contest costs of *Sus scrofa*. Frontiers in Zoology 19, 13.
Camerlink, I., Turner, S.P., Ursinus, W.W., Reimert, I., Bolhuis, J.E., 2014. Aggression and affiliation during social conflict in pigs. PloS one 9, e113502.
Cameron, E.Z., Setsaas, T.H., Linklater, W.L., 2009. Social bonds between unrelated females increase reproductive success in feral horses. Proceedings of the National Academy of Sciences 106, 13850–13853.
Campbell, L.A., Tkaczynski, P.J., Lehmann, J., Mouna, M., Majolo, B., 2018. Social thermoregulation as a potential mechanism linking sociality and fitness: Barbary macaques with more social partners form larger huddles. Scientific Reports 8, 6074.
Chidgey, K.L., 2024. Space allowance for growing pigs: Animal welfare, performance and on-farm practicality. Animal 18, 100890.
Clouard, C., Resmond, R., Prunier, A., Tallet, C., Merlot, E., 2022. Exploration of early social behaviors and social styles in relation to individual characteristics in suckling piglets. Scientific Reports 12, 2318.
Clouard, C., Foreau, A., Goumon, S., Tallet, C., Merlot, E., Resmond, R., 2024. Evidence of stable preferential affiliate relationships in the domestic pig. Animal Behavior 213, 95–105.
Cordoni, G., Comin, M., Collarini, E., Robino, C., Chierto, E., Norscia, I., 2023. Domestic pigs (*Sus scrofa*) engage in non-random post-conflict affiliation with third parties: cognitive and functional implications. Animal Cognition 26, 687–701.
Glickman, M.E., 1999. Parameter estimation in large dynamic paired comparison experiments. Journal of the Royal Statistical Society Series C: Applied Statistics 48, 377–394.
Goumon, S., Illmann, G., Leszkowová, I., Dostalová, A., Cantor, M., 2020. Dyadic affiliative preferences in a stable group of domestic pigs. Applied Animal Behaviour Science 230, 105045.
Goumon, S., Jowett, S., Khatiwada, S., Camerlink, I., 2025. Peer social bonds in farm animals. Animal 19, 101687.
Horback, K., 2014. Nosing around: play in pigs. Animal Behavior and Cognition 2, 186.
Jensen, P., 1980. An ethogram of social interaction patterns in group-housed dry sows. Applied Animal Ethology 6, 341–350.
Jowett, S.L., Silk, M.J., Lee, V., Turner, S.P., Camerlink, I., 2025. Characterising nosing behaviours in pigs after mixing using social network analysis. Animal 19, 101585.
Kaiser, H.F., 1960. The application of electronic computers to factor analysis. Educational and Psychological Measurement 20, 141–151.
Kassambara, A.; Mundt, F., 2016. Package "factoextra" for R: extract and visualize the results of multivariate data Analyses. Retrieved on 20 October 2025 from: https://rpkgs.datanovia.com/factoextra/index.html.
Kappeler, P.M., Clutton-Brock, T., Shultz, S., Lukas, D., 2019. Social complexity: patterns, processes, and evolution. Behavioral Ecology and Sociobiology 73, 5.

Khatiwada, S., Seddaiu, P., Jaszczyk, A., Camerlink, I., 2025a. Is social support mediated by social relationship strength in pigs? Animal 19, 101693.
Khatiwada, S., Lee, V., Turner, S.P., Camerlink, I., 2025b. Trade-offs between proximity and physical contact during group integration in pigs (*Sus scrofa* domesticus). Current Zoology, Published online by Oxford Academic Press 18 August 2025.
Kristensen, H.H., Jones, R.B., Schofield, C.P., White, R.P., Wathes, C.M., 2001. The use of olfactory and other cues for social recognition by juvenile pigs. Applied Animal Behaviour Science 72, 321–333.
Lanthony, M., Danglot, M., Špinka, M., Tallet, C., 2022. Dominance hierarchy in groups of pregnant sows: characteristics and identification of related indicators. Applied Animal Behavior Science 254, 105683.
Lee, V.E., Arnott, G., Turner, S.P., 2022. Social behavior in farm animals: applying fundamental theory to improve animal welfare. Frontiers in Veterinary Science 9, 932217.
McCort, W.D., Graves, H.B., 1982. Social dominance relationships and spacing behavior of swine. Behavioural Processes 7, 169–178.
McGlone, J.J., Curtis, S.E., 1985. Behavior and performance of weanling pigs in pens equipped with hide areas. Journal of Animal Science 60, 20–24.
Meese, G.B., Ewbank, R., 1973. The establishment and nature of the dominance hierarchy in the domesticated pig. Animal Behaviour 21, 326–334.
Meynhardt, H., 1982. Schwarzwildreport. Mein Leben Unter Wildschweinen. Neumann- Neudamm, Melsungen, Germany.
Newberry, R.C., Wood-Gush, D.G.M., Hall, J.W., 1988. Playful behaviour of piglets. Behavioural Processes 17, 205–216.
Newberry, R., Swanson, J., 2001. Breaking social bonds. In: Social Behavior in Farm Animals. CABI Publishing, Wallingford, UK, pp. 307–331.
Petherick, J.C., Blackshaw, J.K., 1987. A review of the factors influencing the aggressive and agonistic behaviour of the domestic pig. Australian Journal of Experimental Agriculture 27, 605–611.
R Core Team, 2025. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Rault, J.L., 2012. Friends with benefits: social support and its relevance for farm animal welfare. Applied Animal Behaviour Science 136, 1–14.
Rault, J.L., 2019. Be kind to others: prosocial behaviours and their implications for animal welfare. Applied Animal Behaviour Science 210, 113–123.
Reimert, I., Bolhuis, J.E., Kemp, B., Rodenburg, T.B., 2014. Social support in pigs with different coping styles. Physiology & Behavior 129, 221–229.
Seddaiu, P., Turner, S.P., Camerlink, I., 2024. Cross-seasonal and diurnal variation in physical contact between sub-adult pigs. Applied Animal Behaviour Science 278, 106379.
Seddaiu, P., Turner, S.P., Camerlink, I., 2025. Long-term social preferences in a group of sub-adult female pigs. Livestock Science 302, 105826.
Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., Cheney, D.L., 2010. Strong and consistent social bonds enhance the longevity of female baboons. Current Biology 20, 1359–1361.
Snyder-Mackler, N., Burger, J.R., Gaydosh, L., Belsky, D.W., Noppert, G.A., Campos, F. A., Bartolomucci, A., Yang, Y.C., Aiello, A.E., O'Rand, A., Harris, K.M., Shively, C.A., Alberts, S.C., Tung, J., 2020. Social determinants of health and survival in humans and other animals. Science 368, eaax9553.
Steinerová, K., Parker, S.E., Brown, J.A., Seddon, Y.M., 2024. The promotion of play behaviour in grow-finish pigs: the relationship between behaviours indicating positive experience and physiological measures. Applied Animal Behaviour Science 275, 106263.
Stephenson, A., Sonas, J., 2012. PlayerRatings: dynamic updating methods for player ratings estimation. R package (Version 1.1-0). Retrieved on 14 February 2025 from: http://CRAN.R-project.org/package=PlayerRatings.
Tabachnick, B.G., Fidell, L.S., Ullman, J.B., 2007. Using Multivariate Statistics. Pearson, Boston, MA, USA.
Taborsky, B., Oliveira, R.F., 2012. Social competence: an evolutionary approach. Trends in Ecology & Evolution 27, 679–688.
Tan, S.S.L., Shackleton, D.M., Beames, R.M., 1991. The effect of mixing unfamiliar individuals on the growth and production of finishing pigs. Animal Science 52, 201–206.
Val-Laillet, D., Guesdon, V., von Keyserlingk, M.A., de Passillé, A.M., Rushen, J., 2009. Allogrooming in cattle: Relationships between social preferences, feeding displacements and social dominance. Applied Animal Behaviour Science 116, 141–149.
Weller, J.E., Camerlink, I., Turner, S.P., Farish, M., Arnott, G., 2019. Playful pigs: early life play-fighting experience influences later life contest dynamics. Animal Behaviour 158, 269–279.
Whitehead, H., James, R., 2015. Generalized affiliation indices extract affiliations from social network data. Methods in Ecology and Evolution 6, 836–844.
Zupan, M., Rehn, T., de Oliveira, D., Malovrh, Š., Keeling, L., 2019. Individual play patterns stimulated by a familiar object are group-driven. Scientific Reports 9, 6092.