Department for Farm Animals and Veterinary Public Health

University of Veterinary Medicine

Institute of Animal Welfare Science

Head: Univ.-Prof. Jean-Loup Rault

Social bonds in pigs

Master thesis

University of Veterinary Medicine

Interdisciplinary Master in Human and Animal Interactions

Master thesis submitted for the fulfilment of the requirements for the degree of

Master of Science (MSc)

Submitted by

Katharina Scheck, BSc

Vienna, September 2020

Supervisors:

Dr. Irene Camerlink

Univ.-Prof. Jean-Loup Rault

Independent evaluator:

Dr. Claudia Bieber

Table of content

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst und keine anderen Hilfsmittel als die angegebenen verwendet habe. Insbesondere versichere ich, dass ich alle wörtlichen und sinngemäßen Übernahmen aus anderen Quellen als solche kenntlich gemacht habe.

Hereby, I declare that I wrote this work independently without outside help and did not use any tools other than those indicated. In particular, I assure that I have identified all the literature and corresponding wording other than such.

…5.August 2020… ..……………………

Date Katharina Scheck

Acknowledgements

I would like to express my deepest gratitude to all the people supporting and contributing to my master thesis.

First of all, I would like to thank Dr. Irene Camerlink for being the best imaginable supervisor, for teaching and guiding me, for sharing her passion, deepening my enthusiasm for welfare science, for being so patient and providing hope in my deepest struggles, and not to forget all the chocolate support, when it was needed the most.

Then I would like to thank Univ.-Prof. Jean-Loup Rault for his great and critical input, the many improving suggestions and his guidance and supervision of this study.

Further I would like to thank Tasha Cadman for collecting data with me and her contribution to the study. Without her, it would never have been so much fun.

This study would also not have been possible without the help and care provided by the staff of Medau – Dr. Doris Verhovsek, Silvia, Tamara and Nico.

Finally, I would like to thank my family and friends for their constant support and believing in me, even when I was struggling.

1. Introduction

Positive social relationships in humans are known to have a positive effect on the physical and mental health of the individual (Smith & Christakis, 2008; Yang et al., 2016). Social relationships are referring to the content, pattern and quality of interactions between two individuals (Hinde, 1976). Apart from humans, other species also form social relationships, which are important for living in complex social structures (Val-Laillet et al., 2009). Different species show preferential associations, where an individual prefers a specific individual over another (Cameron et al., 2009; Durrell et al., 2004; Val-Laillet et al., 2009). If this preference continues over a period of time, some scientist would call this "friendship", whereas this term is critical to use within non-human species (Massen et al., 2010). Another common term, to describe long-term relationships is social bonds. Social bonds can be defined as long lasting, mutual, affectionate and emotional attachment between two specific individuals and are characterized by affiliative behaviours directed towards each other (Newberry & Swanson, 2001). Species-specific affiliative behaviours can therefore be seen as an indicator of social bonds, like allo-grooming, lying in body contact, playing, synchronizing behaviour, maintaining proximity, reinstatement behaviour when separated, and greeting following temporary separations (Silk et al., 2006; Val-Laillet et al., 2009; Wolter et al., 2018). Social bonds are postulated to improve the fitness of the individuals (Armitage & Schwartz, 2000; Cameron et al., 2009; Schülke et al., 2010). In primates social bonds and their benefits on welfare are already well studied (Haunhorst et al., 2017; Lonsdorf et al., 2014; McFarland et al., 2017; Newton-Fisher & Lee, 2011; Silk et al., 2006, 2010). Studies that measured glucocorticoid levels showed that a strong and stable social bond in primates can reduce psychological stress and can further improve their individual fitness (Crockford et al., 2008; Wittig et al., 2008). To understand the undergoing mechanisms, and to try to assess social relationships, a composite sociality index (CSI) has been used especially in primates (Fischer et al., 2017; Silk et al., 2006). In primates the CSI is based on spatial proximity and allo-grooming of the individuals (Silk et al., 2006), but essentially it combines multiple behaviours that happen between two individuals into a single index value.

Many domestic animals are also social species that naturally live in stable social groups and are able to build social bonds. In horses social bonds are able to increase reproductive success (Cameron et al., 2009). It has been shown that farm animals like cattle (Val-Laillet et al., 2009) and sheep (Arnold et al., 1981) also have preferential associations. However, there is a lack of knowledge about how these social bonds can benefit animal's health and other welfare aspects.

Different findings showed, that pigs are able to form preferential associations (Durrell et al., 2004; Podgórski et al., 2014). The ancestor of domestic pigs, the wild boar (*Sus scrofa*), lives in social, stable groups, consisting of two to four related, mature sows and their offspring (Graves, 1984; Meynhardt, 1982). To maintain stability in these groups, wild boars have a dominance hierarchy. Under commercial conditions, pigs establish this hierarchy by prior fights and aggression (Manning & Dawkins, 2012; Peden et al., 2018). Once the hierarchy is established, agonistic behaviour becomes rare (Meese & Ewbank, 1973). Therefore, stable social groups and the possibility to build social bonds could reduce aggression. However, the knowledge about the natural social behaviour in pigs is hardly taken into account in conventional farming. For example the frequent regrouping of pigs, whose resulting aggression can lead to a major welfare issue (Arey & Edwards, 1998). Under this perspective, it is reasonable to further investigate social bonds in pigs to potentially improve the animals' welfare.

When interacting with each other, pigs can show different affiliative behaviours: social play behaviour (Horback, 2014), nose-to-nose contact, allo-grooming (Meynhardt, 1982) and lying in contact (Newberry & Swanson, 2001). Nose-to-nose contact may have an essential role in facilitating a bond between individuals (Newberry & Wood-Gush, 1986). This nose contact not only occurs frequently in the first few days of a piglet's life to define a bond with the mother (Jensen et al., 1991) but also continues later on (Portele et al., 2019). Social grooming is not very frequently performed by pigs (Petersen, 1994). It occurs mostly in mature sows, and in wild boars, where piglets around eight weeks start copying the behaviour (Meynhardt, 1982).

Social bonds in pigs are hardly studied so far. A few studies (Durrell et al., 2004; Goumon et al., 2020) show that they are capable of forming preferential associations. Durrell et al. (2004) investigated pigs in a stable group that form non-random associations by studying their spatial proximity. Goumon et al. (2020) used lying proximity to assess their capability of forming preferential associations. A study performed by Podgórski et al. (2014) identified that wild boars formed non-random preferential associations by assessing their spatial proximity. Some of the pairs even spent over half of their time together. Nevertheless, all these studies only used spatial proximity as their sole indicator to investigate social bonds in pigs, possibly disregarding other important information of the social behaviour of pigs.

The aim of this current study was to record affiliative behaviours and spatial proximity as indicators of social bonds, and to assess whether their integration in a composite sociality index reflects a putative social bond. To assess this, we studied the proximity and affiliative behaviours between individuals and looked at these measures separately as well as combined into a composite sociality index.

2. Material & Methods

All methods and animal use within this study were approved by the institutional ethics committee of the University of Veterinary Medicine, Vienna (ETK-04/01/2019).

2.1.*Animals and Housing*

The study took place at the pig research and teaching farm 'Medau' of the University of Veterinary Medicine, Vienna, Austria. Twenty-three healthy sows and their litters, in total 283 piglets, were used for this study. Purebred Large White sows farrowed over two batches that were five weeks apart. Sows were mainly in their fourth (30%) or second parity (26%), and the remaining sows were in their third (13%), fifth (13%), seventh (9%), sixth (4%), or eight parity (4%). From farrowing to weaning sows and their piglets were housed in BeFree farrowing pens (Schauer Agrotronic GmbH, Prambachkirchen, Austria). The BeFree pen size was 2.22 m × 2.86 m (sow movement area of $4.2m^2$) with plastic slatted floor and a concrete lying area. The temporary crating system was not used before, during or after farrowing, except for short-term safe handling of the sow and piglets. Sows were fed dry commercial sow feed (pellets) at 7:00, 11:30 and 15:30 h and received hay daily in a rack. The piglets had a covered and heated creep area of 1.25 m × 0.61 m, one drinker (ad libitum water) and received a commercial piglet feed (pre-starter meal) from seven days of age. Lights were on between 07:00 and 16:00 h and the temperature was set at 20°C. Average litter size at birth was 14.3 piglets (range 2–19). Cross-fostering was applied if the number of piglets exceeded the number of functional teats of the sow, occurring within the first 72 hours post-partum. There were 145 male (51%) and 138 female (49%) piglets. Within 48 hours after birth, piglets' teeth were grinded (to prevent facial injuries due to fighting at the udder), and each piglet was weighed and marked with a non-invasive tail mark using Kinesiology tape. The tape was cut to be 5 cm long and 1.5 cm wide for double coloured and 3 cm wide for single coloured tags and was placed 1 cm from the base of the tail (Figure 1). Males were castrated around two weeks of age under general anaesthesia. The piglets were ear-tagged at approximately 19 days of age and vaccinated.

Figure 1. Coloured tail marking for identification.

Piglets were weaned at 25.94 ± 1.18 days of age. After weaning 78 piglets from batch 1 and 52 piglets from batch 2 were further studied, based on their sociality index. Focal piglets were selected and paired with one familiar littermate, which was either a high or low index scoring partner. Batch 1 was weaned into eight pens of 8 – 10 piglets each and batch 2 was weaned into four pens of 12 – 14 piglets each. The weaning pens measured 3.1 × 4.7 m with concrete and 45.5% slatted floor. Each pen included a covered, heated creep area of 1 × 3 m, in which straw or wood shavings were provided as bedding material. Each pen had a round multi-space feeder with ad libitum commercial piglet meal diet and four drinkers. Temperature was regulated through fans and a wall curtain on each side of the room. Average room temperature was in the first batch 21.56±1.38°C (range 20.2 – 25.5°C) and in the second batch 22.67±1.38°C (range 21.8 – 25.5°C).

2.2.*Behavioural observations*

Affiliative and agonistic behaviours were recorded using the ethogram shown in Table 2, while noting the actor and recipient of the social behaviour. Behavioural observations were performed using the Animal Behaviour Pro App, version 1.2 (University of Kent, Canterbury, UK) with the ‘ad libitum’ recording function. Live behavioural observations were conducted by two observers pre-weaning once a week (days 4, 11, and 19 postpartum) and just after weaning (day 27) for three consecutive days (days 28, 29 and 30). A final day of behavioural observations was recorded three weeks post weaning (day 47) to assess the groups after a socially stable phase.

Week	1	2	3	4	5	6	7	8	9	10	11
Batch1	Birth Obs.	Obs.	Obs.	Wean Obs.			Obs.				
Batch2					Birth Obs.	Obs.	Obs.	Wean Obs.			Obs.

Table 1. Timeline of live behavioural observations.

Observations were carried out for 5 h per day between 10:30 – 12:30 h and 13:00 – 16:00 h using scan sampling. Pre-weaning, two-minute scans were used for observations per pen, resulting in 25 scan samples per pig per day (in total 75 scan samples per pig pre-weaning). Post weaning, five-minute scans were used per four pens, resulting in 60 scan samples per pig per day (in total 240 scan samples per pig post weaning). Piglets were marked with a marker pen (pre-weaning) or animal marker spray (post weaning) on their back in the morning before each observation for better identification. The observations started at least 30 minutes after the marking to ensure that the behaviour of the pigs was not influenced by the marking process. Observers rotated between the pens for observations.

Behaviour	Description
Nose-to-nose contact	Pig's nose disc or snout makes physical contact with snout or nose disc of another piglet.
Allo-grooming	Pig gently nibbles or licks the face (may include the snout, ear, and eye region, including lashes) or body of another without causing acute skin damage to the recipient.
Other affiliation	Pig is nosing the face of another piglet; is engaged in social play; or is jointly exploring whereby their heads are in proximity whilst engaged in an activity.
Agonistic behaviour	Pig is engaged in fight; bite; head knock; play fight (pig alternates displays of both play and agonistic elements, without causing injury to the partner); threat.
Other	All other behaviour

Table 2. Ethogram for given or received affiliative behaviours in pigs.

In total, 285 piglets (140 females, 145 males) were studied pre-weaning. The average litter size at birth was 14 ± 2 piglets (range 11 – 18). The average birth weight was 1.56 ± 0.35 kg (range 0.72 – 2.59 kg) and did not differ between males (1.59 ± 0.03 kg) and females (1.53 ± 0.03 kg) ($P = 0.33$). Fourteen percent ($n = 41$) of all the piglets were fostered to another litter prior to the first observations. Fostered piglets (13 females, 28 males) were on average lighter at birth than non-fostered piglets (foster: 1.49 ± 0.05 kg, non-foster: 1.57 ± 0.02 kg; $P < 0.001$). Due to mortality and fostering, the average number of piglets per litter at weaning was 11 ± 1 (10 – 13).

At weaning, 132 of those pigs (62 females, 65 males) were relocated to weaning pens, where they were housed in groups of on average 10 pigs (range 7 to 13). The average weight at weaning was 7.6 ± 1.76 kg (range 2.63 – 11.60 kg). Weaning weight did not differ between males (7.37 ± 0.40 kg) and females (7.33 ± 0.38 kg) ($P = 0.89$). From the 41 fostered piglets pre-weaning, 10 of those pigs were also studied after weaning (4 females, 6 males). Fostered pigs did not differ in their body weight at weaning from non-fostered pigs (foster: 7.05 ± 0.68, non-foster: 7.64 ± 0.18; $P = 0.40$).

2.3.Nearest neighbour proximity

Proximity was recorded by noting the nearest neighbour when pigs were lying down (either inactive or sleeping), for at least 10 observations per pig per week for weeks 1 – 4 and week 7 of life using the Animal Behaviour Pro App with the 'ad libitum' function. This resulted in total in 8103 observations on proximity. The pen walls were marked at 50 cm intervals to allow distance measurements. Proximity was recorded when at least half of the piglets were lying down, with at least 30 minutes between observations or when the piglets had changed location. It was differentiated between pigs lying in full body contact, part body contact or at distance to each other and if they were lying in a head-to-head or head-to-tail position (Table 3). Each neighbour was recorded as a single entry, resulting in multiple entries when, for example, a pig was sleeping in body contact with three others (this was then counted as one observation).

Proximity	Description
Full body contact	Lying with a minimum of 75% of body against neighbour
Part Body Contact	Lying with 25 – 74% body against neighbour
Nearest Neighbour <0.5 m	Lying with <24% body against neighbour or within 0.5 m of neighbour
Nearest Neighbour >0.5 m	Lying >0.5 m but <1 m from neighbour
Nearest Neighbour >1 m	Lying >1 m from neighbour

Table 3. Ethogram of proximity and orientation towards the nearest neighbour.

2.4. Sociality Index

Prior to weaning, the sociality index was calculated for each piglet, based on the composite sociality index (CSI, Silk et al., 2006; Cameron et al., 2009):

$$\frac{\left(\frac{Gij}{Gxy}+\frac{Pij}{Pxy}\right)}{2}$$

The equation above takes the average (sum divided by two) of the frequency of affiliative behaviour (allo-grooming – G_{ij}) and proximity (P_{ij}) per dyad divided by the respective average frequency of the group conducting the same behaviour (G_{xy}, P_{xy}). As pigs do not show much grooming, all affiliative behaviours including grooming were summed for the frequency of affiliative behaviours. To calculate the index, the proportion of affiliative behaviours per pair (nose-nose contact, allo-grooming, other affiliation given and received summed) was calculated for each individual by dividing the number of affiliative interactions of each pair by the total number of affiliative interactions of the individual. The index of both individuals is then summed up, so that it gives a better reflection of all interactions between the pair. Using the proportion of interactions between a pair adjusts for the difference in frequency of affiliative behaviours shown. The proportion is then divided by the litter size (pre-weaning) or group size (post weaning) to get the affiliative behaviours per pair adjusted for the number of animals in a group, as this results in different numbers of possible interaction partners between groups. The value was then divided by the average of the study population. The same procedure was done for the proximity between each possible dyad combination. The two proportions were averaged (summed and divided by two) to get the final sociality index for each focal pig of a pair. Hereby the values are scaled with an average of 1. As the observations were recorded by focal animal, the interactions were counted for both pigs in each dyad (e.g. interactions from A to B and B to A) were summed. This resulted in a sociality index by dyad, with an average value of 2.

For each individual the percentage of strong associations with its pen mates was calculated as the number of associations with an index >2, divided by the number of pen mates. Similarly, the percentage of weak associations (individual index <0.5) was calculated for each individual. The strongest association, out of each individual's interactions, was recorded by individual. The weakest association was excluded as this resulted in many zeroes. These three variables were obtained for the index made pre-weaning, at weaning and at three weeks post-weaning.

2.5.Data Analysis

The inter-observer reliability from the two live observers was calculated with BORIS v7.7.3 (Friard and Gamba, 2016) using a Cohen's Kappa test (average K = 0.755). Statistical analyses were performed using the software packages R, version 3.6.0. (R Core team, Vienna) and SAS, version 9.4 (Statistical Analysis Software, SAS Institute, USA).

Differences in affiliative behaviours and proximity between different observation weeks were analysed using a linear mixed model and the focal pig as repeated variable when analysed across multiple days, whereas sow and weaning pen were used as random variables. Sex and whether pigs were fostered or not and week of life were included as fixed effects. Nosing and grooming behaviour was not normally distributed, therefore it had to be analysed for the sociality index as all affiliative behaviours together (of which the model residuals were normally distributed). The interaction between body weight and fostering was taken into account in all models pre-weaning.

For the sociality index the response variables (number of strong and weak associations, and strongest association) were analysed in mixed models using sex (male or female), fostered (yes or no), the number of pen mates, and body weight at birth as predictor variables for analyses pre-weaning, or body weight at weaning for the analyses at weaning and post-weaning. The random variable was pen, nested within batch. All model residuals were normally distributed.

3. Results

3.1.Affiliative behaviours

The percentage of observations spent on nose-to-nose contact, grooming and other affiliative behaviours (including nosing head, social play and joint exploration) summed in total, on average, in 9.66 ± 0.212 % (range 0 – 63%) of the total observations (in 90.34% of the time pigs performed other behaviour, including active behaviour and resting, when not interacting with another pig). Nose-to-nose contact and allo-grooming increased in the 7th week of life as compared to the first four weeks of life (P <0.01) (Figure 2). The percentage of other affiliative behaviours was significantly lower in week 1 and week 4 as compared to week 2, 3 and 7 (P <0.001) whereas the difference between week 1 and 7 was a tendency (P = 0.07). There was no effect of the piglet's sex or whether it was fostered or not on the total amount of affiliative behaviours (nosing, grooming and other summed; P > 0.10).

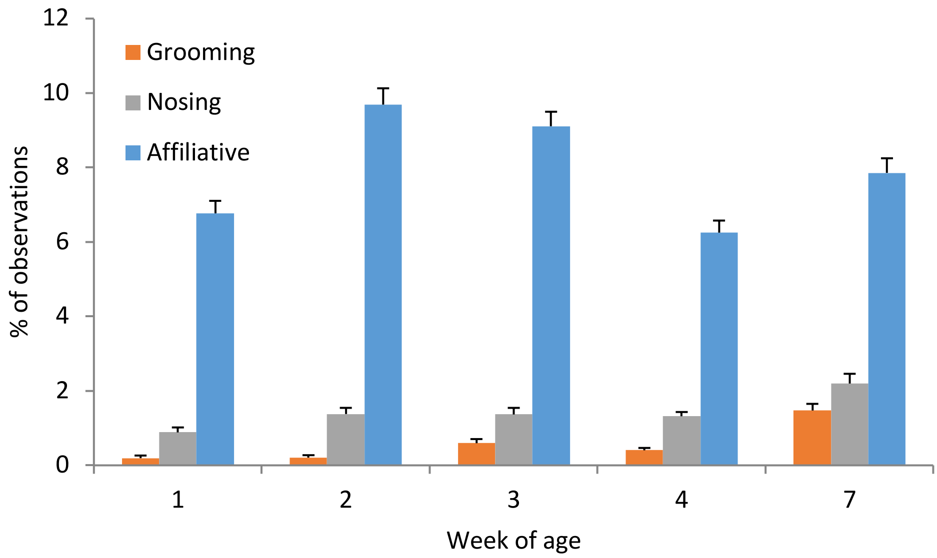

Figure 2. The average percentage of observations (behavioural scans) spent on nose-to-nose contact, grooming and other affiliative behaviours, by week of age.

3.2.Proximity

In total, 8103 observations on proximity were made. In 46.2% of the observations pigs were lying in full body contact to another, of which in 32.7% with the heads together and 13.5% head-to-tail directed (Figure 3). In 44.6% of the observations pigs were lying partly in body contact to another, of which 21.4% with the heads together and 23.2% of the times head-to-tail. In 7% of the observations they were lying within less than 0.5 m distance from another

(3.1% head-to-head; 3.9% head-to-tail) and lying more than 0.5 m away from another was observed only in 2.2% of the observations (1.2% at 0.5-1m; 1% at >1m). Overall, the percentage of observations that the pigs were lying in full body contact differed between the weeks (P <0.001), whereby pigs were significantly more lying in full body contact in week 3 and 4 than in the other weeks, with the lowest percentage of lying in body contact in week 7. The percentage of lying partly in body contact did not differ across the weeks (P = 0.87). The orientation of lying with the heads together (head-to-head-position) did not significantly differ between the weeks (P = 0.63).

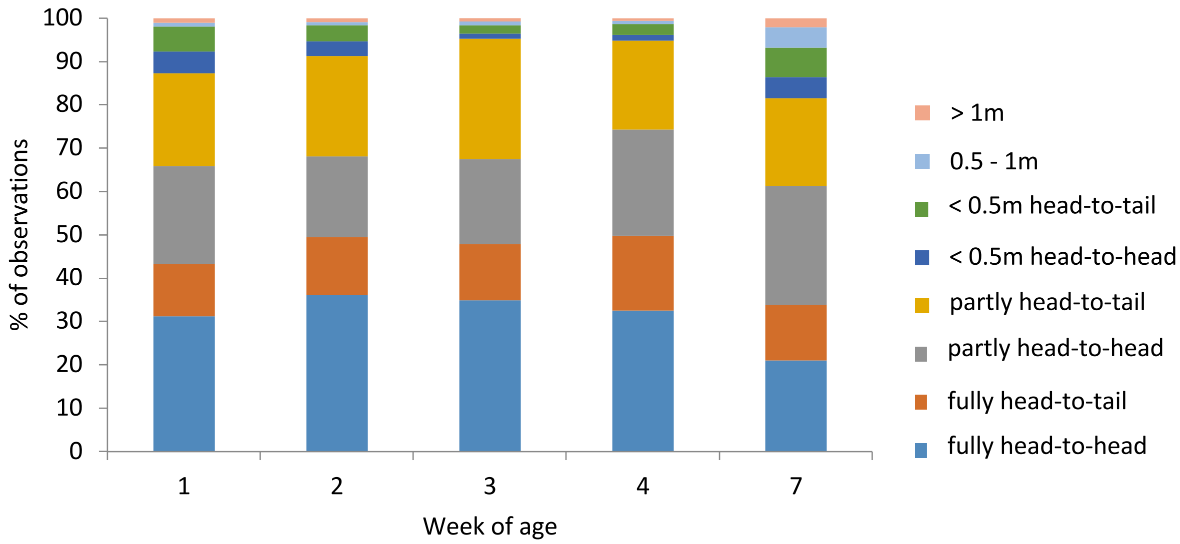

Figure 3. Proximity to the nearest neighbour, in percentage of observations by week.

3.3. Sociality index pre-weaning

The sociality index pre-weaning was based, on average, on seven observations per pig of affiliative behaviours and, on average, 23 observations per pig of proximity.

The index based on the observations of affiliative behaviours ranged from 0 to 17.32. There were 698 dyads (out of 1632 possible dyads pre-weaning; 42.8%) that did not show affiliative behaviours towards each other during the observations. Out of the dyads that did interact, 274 (16.8%) had an index below average (<2) and 660 (40.5%) had an index above average, of which 285 (17.5% of total) had an index of >4 (twice the average). The index based on the proximity only ranged from 0 to 11.45. There were 51 dyads in which the pigs were not lying next to each other during the observations (3.1%). Of the dyads that did lie in proximity, 801 (49.1%) dyads had an index below average and 780 dyads an index above average, of which

59 (3.6%) had an index >4. The index of affiliative behaviours did not correlate with the index of proximity (r = 0.21; P = 0.40).

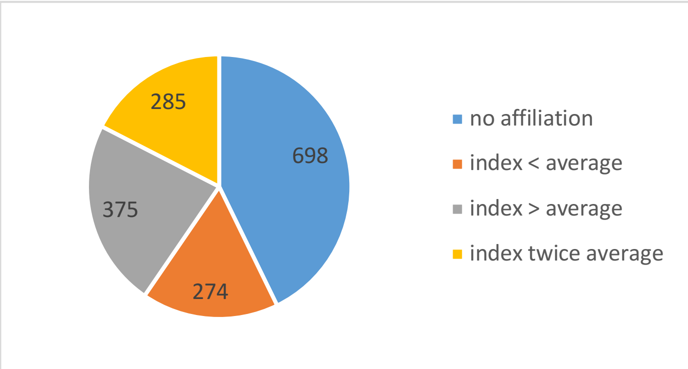

Figure 4. Numbers of dyads based on affiliative behaviours pre-weaning.

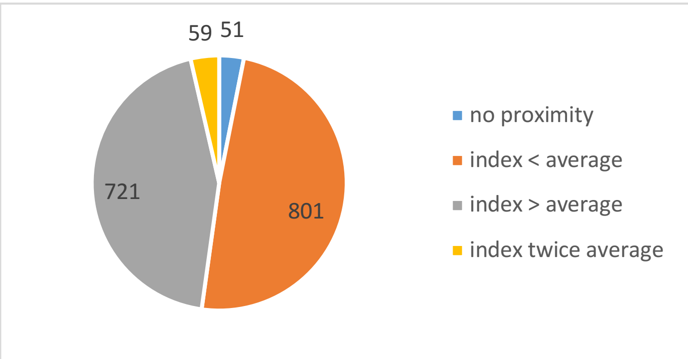

Figure 5. Numbers of dyads based on proximity pre-weaning.

The average sociality index had a minimum of zero and a maximum of 9.69 (Figure 6). Out of the 1632 dyad combinations before weaning (i.e. interactions between pairs of pigs), only 25 littermate pairs (1.53%) did not interact at all during the behaviour observations nor were they nearest neighbour at any of the observation days across the three weeks. Of the dyads that did interact, 923 (56.6%) had an index below average and 684 had an index above average, of which 142 (8.7%) had a sociality index of twice the average (>4).

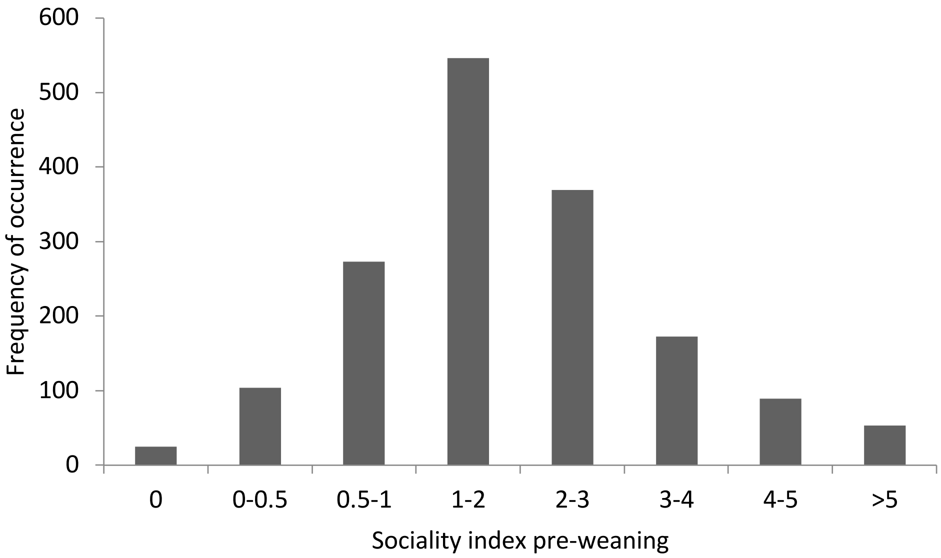

Figure 6. Distribution of the sociality index pre-weaning.

Piglets had pre-weaning on average 33 ± 14% (0 – 75%) weak associations and 11.7 ± 9.2% (0 – 40%) strong associations, with the strongest association (on the individual level) being on average an index of 2.65 ± 0.86 (1.41 – 6.28).

The number of pen mates strongly influenced the percentage of weak associations, with more weak associations in pens with more piglets (b = 4.89 ± 1.57 % / piglet; P = 0.002) and also influenced the percentage of strong associations with a lower percentage of strong associations in pens with more piglets (b = -5.82 ± 0.66; P < 0.001) and a lower strongest index (b = -0.34 ± 0.06; P <0.001).

Body weight and fostering also influenced the percentage of weak associations (P = 0.02), with fewer weak associations in heavier non-fostered piglets (b = -8.0 % / kg) and more weak associations in heavier fostered piglets (b = 5.4 % / kg). Fostered piglets overall tended to have fewer weak associations (foster: 31.0 ± 3.08, non-foster: 32.8 ± 1.66; P = 0.053). Males tended to have fewer weak associations than females (males: 30.5 ± 2.08, females: 33.4 ± 2.16; P = 0.094). Body weight, fostering and sex did not influence the percentage of strong associations and the value of the strongest index per individual (all P>0.10).

3.4.*Sociality index post-weaning*

In the week after weaning, behaviour and proximity was observed on three consecutive days.

The index based on the observations of affiliative behaviours only ranged from 0 to 14.82. There were 168 dyads (out of 657 possible dyads; 25.6%) that did not show affiliative behaviours towards each other during the observations. Of the other dyads that did interact, 224 had an index below average (<2) and 163 had an index above average, of which 102 (15.5% of total) had an index of >4 (twice the average). The index based on the proximity only ranged from 0 to 11.11. There were 136 possible dyads that did not lie in close proximity during the observations (20.7%). Of the dyads that did lie in proximity, 249 dyads had an index below average and 188 dyads an index above average, of which 84 (12.8%) had an index >4.

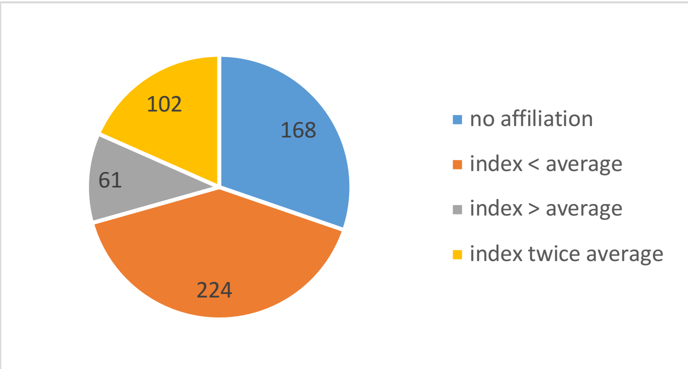

Figure 7. Numbers of dyads based on affiliative behaviours post-weaning.

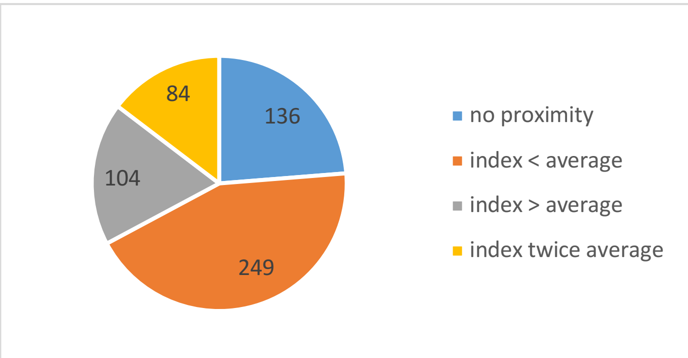

Figure 8. Numbers of dyads based on proximity post-weaning.

The correlation between the index of affiliative behaviours and proximity was $r = 0.13$ (n = 657, P <0.001). The composite sociality index, which is the average of the index for affiliative behaviours and proximity, ranged from 0 to 10.30. There were 35 dyads (5.3%) that did neither show affiliative behaviours nor were lying in close proximity (Figure 8). Of the dyads that did interact, 348 had an index below average and 205 had an index above average, of which 69 (10.5%) had a sociality index of twice the average.

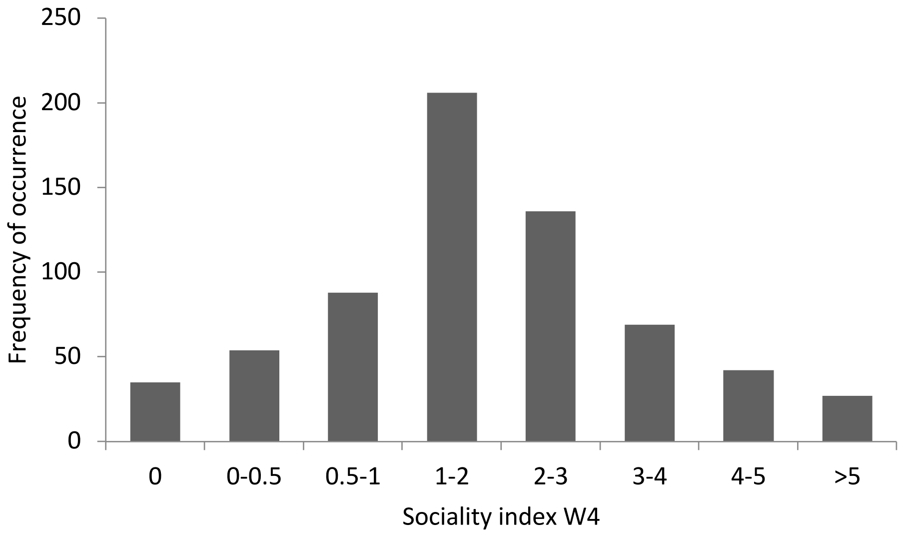

Figure 9. Distribution of the sociality index in the week after weaning for all dyads (n = 657). The average is 2.

In the week of weaning, pigs had on average 32 ± 16% (0 – 85%) weak associations and 15.1 ± 11.9% (0 – 57%) strong associations, with the strongest association being on average an index of 2.77 ± 0.99 (1.08 – 6.37).

The number of pen mates strongly influenced the percentage of weak associations (b = 5.98 ± 0.64; P = <0.001) and strong associations (b = -5.34 ± 0.64; P <0.001) in the week after weaning. The percentage of strong associations was lower when there were more pigs in the pen. (b = -0.37 ± 0.05; P <0.001).

In contrast to the pre-weaning situation, males had significantly more weak associations than females in the week of weaning (males: 35.2 ± 2.34%, females: 29.6 ± 2.53%; P = 0.008). The strongest associations was higher in males compared to females (males: 3.06 ± 0.16, females: 2.72 ± 0.16; P = 0.01), suggesting that males make fewer strong associations but that the associations that do exist are stronger than in females.

Fostering did not influence the percentage of weak associations and strong associations (weak: P = 0.72, strong: P = 0.93), the same is true for body weight (weak: P = 0.16, strong: P = 0.66). Fostering (P = 0.36) did not influence the strength of the association, and body weight had no significant effect and was omitted from the model.

3.5.*Sociality index in stable groups*

In week 7, three weeks after weaning, the sociality index was calculated again for the same groups.

The index of affiliative behaviours only ranged from 0 – 14.36. There were 247 dyads (37.6%) that did not show affiliative behaviours towards each other during the observations. From the interacting dyads, 142 had an index below average and 151 had an index above average, of which 117 (17.8% of total) had an index of >4. Based on the proximity only, the average index ranged from 0 – 17.76. There were 226 dyads that did not lie together as nearest neighbours (34.4%). Of the dyads that did lie in proximity, 199 dyads had an index below average and 144 dyads an index above average, of which 88 (13.4%) had an index >4. There was a weak correlation between the index of affiliative behaviours and proximity r = 0.19 (n = 657 dyads, P <0.001).

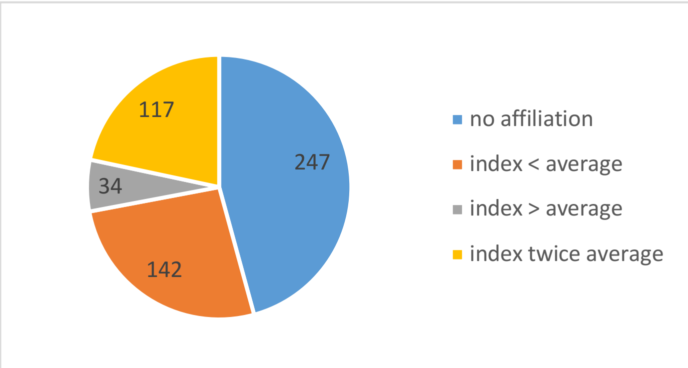

Figure 10. Numbers of dyads based on affiliative behaviours week7.

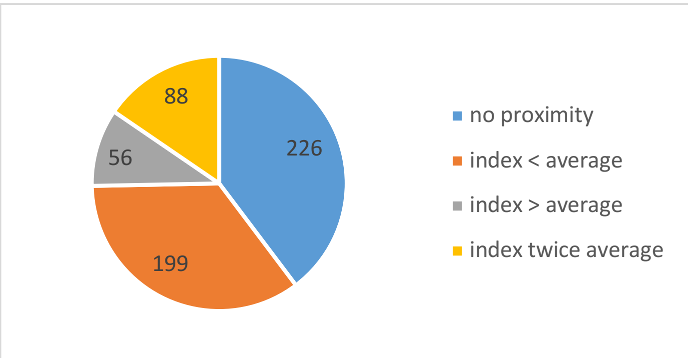

Figure 11. Numbers of dyads based on proximity week7.

The average composite sociality index ranged from 0 – 12.52. There were 96 dyads (14.6%) that did neither show affiliative behaviours nor were lying in close proximity (Figure 11). Of the other dyads, 304 had an index below average and 180 had an index above average, of which 77 (11.7%) had a sociality index of twice the average.

The sociality index in the week after weaning was only weakly correlated with the sociality index in week 7 (r = 0.19; P <0.001).

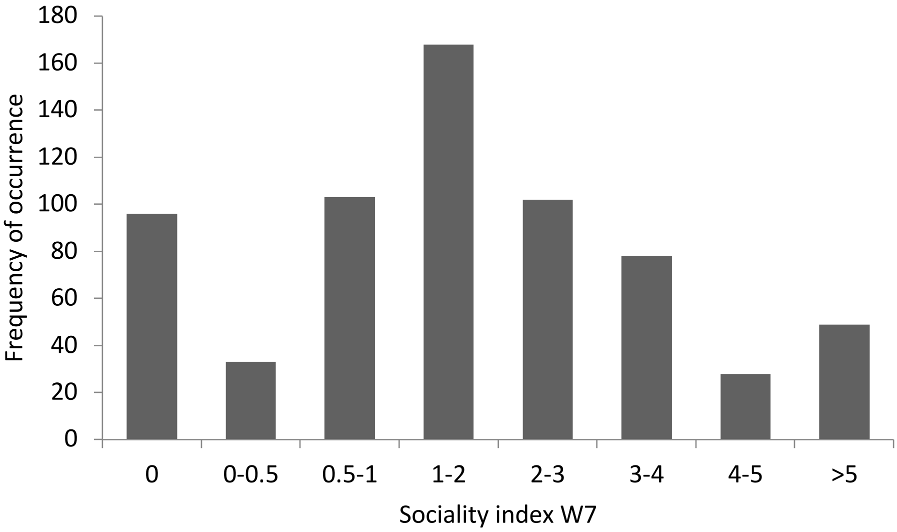

Figure 11. Distribution of the sociality index in week 7, 3 weeks after weaning.

The average percentage of weak associations was 41.2 ± 16.5 (range 0 – 85.7) %, the average percentage of strong associations 15.2 ± 12.3% (0 – 44.4%), and the strongest association was on average 3.40 ± 1.78 (1.05 – 10.02).

The percentage of weak associations was greater in males than in females (males: 43.8 ± 3.86%, females: 37.3 ± 4.15%; $P = 0.03$), and was at this time not significantly influenced by the number of pen mates ($P = 0.61$), fostering ($P = 0.88$) and body weight at weaning ($P = 0.98$).

The percentage of strong associations was lower when there were more pigs per pen ($b = -4.57 \pm 0.75$; $P < 0.001$), but was uninfluenced by the pigs' sex ($P = 0.55$), fostering ($P = 0.49$) or body weight ($P = 0.19$). The strongest association was lower in pens with more pigs ($b = -0.65 \pm 0.11$; $P < 0.001$), but was uninfluenced by sex ($P = 0.21$), fostering ($P = 0.16$) and body weight ($P = 0.32$).

4. Discussion

The main objective of this study was to examine affiliative behaviours and spatial proximity as indicators of social bonds, and to assess whether their integration in a sociality index reflects a putative social bond. To this end, lying in proximity and affiliative behaviours of pigs were observed and a sociality index for each possible dyad was calculated. Results showed that 15.5% of all pig dyads show a sociality index even twice above average. These outcomes suggest that some pigs seem to form social bonds.

4.1.*Affiliative Behaviours*

Affiliative behaviours can be linked to building and strengthening social bonds between group mates and can reduce aggression (Boissy et al., 2007). In pigs it includes nose-to-nose contact, allo-grooming and other affiliative behaviours. Across all observations, pigs performed affiliative behaviours in about 10% of the behavioural scans. The noticeable amount of affiliative behaviour is also in line with what is presented in the literature (Gonyou, 2001; Newberry & Wood-Gush, 1986). There was a significant decrease in affiliative behaviour in week one and week four, when compared to week two, three and seven. A reasonable explanation for this outcome could be that in their first week of life piglets mainly eat and sleep, and barely interact with their siblings (Fraser, 1978; Newberry & Wood-Gush, 1986; Stanged & Jensen, 1991). Around day eight, they become more active and all social behaviour increases, including affiliative behaviour, as also shown in this study. At week four the piglets were weaned from their mother and regrouped. Weaning represents a very stressful event for the piglets (Campbell et al., 2013) and within a new group, they need to establish a new dominance hierarchy (Meese & Ewbank, 1973). This usually leads to increased fighting and aggression, and to fewer affiliative behaviours (Stookey & Gonyou, 1994). After one week, the hierarchy is mainly established, so affiliative behaviour increases again (Meese & Ewbank, 1973).

Nose-to-nose contact did not occur as much as expected based on reports from other studies (Portele et al., 2019; Stanged & Jensen, 1991). However, these studies only observed piglet to sow nose-to-nose contact, and not the nosing behaviour between littermates. It is likely that in the first weeks of life the bonding with the mother is more important than with the siblings (Stanged & Jensen, 1991) and the older they get, the more they focus on their littermates

(Newberry & Wood-Gush, 1986). This would be an explanation why there is such a big difference in the frequency of nose-to-nose contact to siblings and their mother. Newberry & Wood-Gush (1986) examined the social relationships of piglets in a semi-natural environment. Their work indicated that piglets from birth to 13 weeks of age form the strongest relationship to their littermates, not to their mother. From eight weeks of age on piglets more and more disperse from their mother, which can be associated with weaning (Newberry & Wood-Gush, 1986). Camerlink & Turner (2013) investigated social nosing behaviour between littermates in stable groups after weaning and showed that it has an essential role in their affiliative behaviour. In our study the group was not consistent, and bonds needed to be re-established after weaning. In week seven, when the group composition remained stable, the occurrence of social nosing increased as compared to the weeks before weaning.

Allo-grooming behaviour hardly occurred except for the last observation week. In week seven there was a significant increase in grooming. This finding is in line with what is reported in literature about wild boars (Meynhardt, 1982). It states that piglets with eight weeks of life start to copy the behaviour of the mother sow and groom each other. Nevertheless, in this study the grooming behaviour is not very enduring, and it is sometimes hard to distinguish it from belly-nosing when directed to the abdominal region. However, as weaned pigs grow up without their mother, copying her grooming behaviour is not possible. This could possibly lead to an even later establishment of grooming behaviour in growing pigs.

Considering these outcomes it might not be recommended to use grooming as a separate factor in the sociality index, like it is performed in the research in primates (Silk et al., 2006). Moreover, in primates allo-grooming is strongly related to bond maintenance (Cords, 1997), whereas in pigs grooming might serve a different role within social interaction.

4.2.*Proximity*

Pigs were lying most of the time in body contact to one another. Only in 9.2% of the observations pigs were lying without any body contact. The stocking density in the weaning pens was quite low, with at least 1m^2/animal, whereas the minimal space requirement in Austria for weaned pigs is 0.2m^2/animal, according to §5, 1.THV, 2017 (RIS, 2020). This low stocking density indicates that the individuals lied within body contact by choice as there would have been enough space to disperse further. This is in contrast to the limited space in commercial housing, where pigs are prevented from keeping their personal space.

Not lying in contact was most frequently observed in week seven, when the group composition was stable. This appears rather unexpected at first sight, because lying apart from each other more likely fits to the week of weaning, when they meet unrelated piglets (Turner et al., 2013). Literature suggests that sleeping proximity is strongly influenced by temperature (Bracke, 2011; Huynh et al., 2005; Olczak et al., 2015). As the temperature during this week was above the average (total average temperature was 22.17±1.47°C, in week seven average temperature was 22.88±2.14°C) this could have triggered the desire in pigs to sleep without any body contact. As pigs only have a small amount of sweat glands (Bracke, 2011), they have a wide range of behavioural thermoregulation. Therefore, huddling together especially in the first weeks of life can be linked to a survival instinct for proper heat production. In week 7 pigs are better able to thermoregulate due to a greater body fat deposition, so they do not need the warmth of others to the same extent anymore.

This knowledge needs to be taken into account, when the nearest neighbour proximity is used as an indicator for social bonds, especially if it is the only behaviour that is taken into account. Furthermore, Durrell et al. (2004) questioned how far it can be distinguished if pigs are showing preferential associations or just sharing preferences for the same lying locations. Also Turner et al. (2003) could not prove that the resting location of the focal pigs was dependent on a specific group member. In our study weaned pigs stayed the whole time in the same pen. Therefore, it is not possible to exclude this explanation.

Our data collection of lying proximity also included if pigs were lying head-to-head or head-to-tail oriented. Of all the pigs that were lying in body contact, 54.1% were lying with head towards head and 36.7% with head towards tail. There seems to be a clear preference for head towards head. As nose-to-nose contact has an essential role in their affiliative behaviour (Camerlink & Turner, 2013), it seems reasonable that lying with their noses towards each other has a higher value than looking in the opposite direction. Further investigation is needed to verify this assumption, even though the preference of head towards head promises interesting results.

To gain more information about social relationships with the proximity data, it might be interesting to, apart from only recording the nearest neighbour while lying, also record them while being active. Animals in general show clear preferences for which individual they allow close proximity (McBride, 1971). While active, the dominance hierarchy in pigs influences the distance to the nearest neighbour. It has been shown that dominant pigs keep larger distances to others than subdominant pigs (McCort & Graves, 1982). Another study suggests that in groups of less aggressive pigs, individuals tend to prefer a smaller personal distance (Erhard et al., 1997). Therefore, it would be interesting to see if lying behaviour and spacing behaviour when they are being active correlate with each other, and how this could be introduced in the sociality index.

Another possibility could be that there are different aspects or types of social relationships. One study in humans by Pearce et al. (2017) investigated the association of different social neuropeptides in three separate social domains (disposition, dyadic relationships and social network) and showed that endorphins, oxytocin and dopamine being associated with predominantly a different social domain. This implies that there are probably different types of relationships, each requiring a different kind of measurement to be properly assessed.

4.3.*Sociality Index*

The composite sociality index consists of the frequency of affiliative behaviour and lying in proximity, recorded per dyad. Results of the application of the index suggest that pigs are able to form social bonds. Female and male pigs did not differ consistently in their intensity of forming a social bond, whereas fostered pigs formed a weaker social bond than non-fostered pigs.

To calculate the sociality index, affiliative behaviour as well as lying in proximity were used. This is different to previous studies regarding social bonds in pigs (Durrell et al., 2004; Goumon et al., 2020), where only lying in proximity was taken into account to assess a social bond. However, studies with other species, like primates, in which social bonds have been studied the most, are at least using two behavioural measures: proximity, grooming and/or affiliative behaviour (McFarland et al., 2017; Schülke et al., 2010; Silk et al., 2010). Proximity and grooming behaviour seem to be a reliable measurement of social relationships in primates, because of their validation and correlation between each other (Cords, 1997). However, our current study shows a lack of correlation between affiliative behaviour and proximity, which questions the use of the composite sociality index at least for pigs housed in groups that have limited space allowance. The consideration of grooming and proximity in studies of social relationships has, however, quite a long history, as they were already used in early naturalistic studies of primates (Carpenter, 1965; Lindburg, 1973). These behaviours are characterized by their relatively frequent and long lasting sequences and therefore sufficient data can be obtained from it (Cords, 1997).

As grooming in pigs rarely occurs, spatial association is so far the main parameter to indicate social bonds. Studies have shown that primates that stay in closer proximity show less aggressive behaviour and attend to more sociopositive interaction (Colvin & Tissier, 1985; Fairbanks, 1980; Watts, 1994). This phenomenon is also seen in other species like cows. Spacing behaviour is more common the more familiar cows are (Gygax et al., 2010). This strengthens also the integration of the spacing behaviour in the sociality index. Pigs might not have social relationships as complex as primates, but they still show a variety of positive social behaviour (Gonyou, 2001; Meynhardt, 1982; Newberry & Wood-Gush, 1986), which has been overlooked by only considering their lying proximity behaviour. Whether nose contact can be a substitute for grooming for measuring affiliative behaviour will require further study, as nose contact may also increase when many new social encounters occur (for example at weaning).

Social bonds have so far also been found in other farm animals: In ungulates allo-grooming and food sharing is suggested to be a reliable indicator for a social bond (Wasilewski, 2003). In cattle allo-grooming and spatial proximity were used (Val-Laillet et al., 2009). A study by Wolter et al. (2018), tested different measurements of social indicators in horses. They found out that there was a strong correspondence between mutual grooming and friendly approaching, whereas there was only a weak correspondence between mutual grooming and spatial proximity. Therefore, Wolter et al. (2018) recommended using a combination of proactive behaviours, like mutual grooming and friendly approaches, for the assessment of social bonds in horses. This outcome is in line with the results of our study, as there was only a weak correlation between affiliative behaviour and proximity. This weak correlation either implies that the way the index is used in the study needs to be improved to provide a valid outcome (for example, more data points may be needed) or that in commercially housed pigs there may be no relationship between affiliative behaviour and proximity (for example, due to the limited space allowance).

Nevertheless, the sociality index itself is not sufficient for showing how persistent these relationships are. Therefore, we used a longitudinal approach to compared the social bonds from week four to week seven. During this time frame the group composition was consistent. However, at week four when piglets have just been weaned, most of the group was unfamiliar to each other, hence fewer and weaker bonds would have been expected. The sociality index from week four to week seven only weakly correlated with each other. This implies that relationships in pigs are changing over time, possibly because they were mixed into new groups. This finding is in line with the study from Newberry et al. (1986), where social relationships of piglets in a semi-natural environment were tested. They discovered that pigs form social bonds, which were not persistent over time. One explanation by Newberry et al. (1986) was that this is an adaptive behaviour due to their evolution and the fact that wild boars have had predators and therefore, it was better for their fitness to maintain a good relationship to the whole group and not to concentrate on one specific individual. In conventional farming there is a high mortality rate of piglets especially in large litters (Muns et al., 2016), so presumably that could be a reason why there is not such a strong individual recognition. Another reason that emphasizes their high social adaptability is the formation of their dominance hierarchy. Within 48 hours after being regrouped pigs are able to establish a new dominance hierarchy (Meese & Ewbank, 1973). This indicates that pigs are able to adapt socially very quickly to a new group composition.

Still the sociality index as it has been used in this study has limitations and needs to be seen with caution. The threshold for categorizing a dyad of having either a strong or a weak bond is arbitrary as it is compared to a relative value, applicable only to the specific study population. As research in pig's positive social behaviour is a rather new direction and it was worthwhile to investigate, for the first time, whether the composite sociality index can be adapted to pigs. A main disadvantage is that the outcome is only relative for the population of the two batches that have been investigated and cannot be compared across populations or generalized to other contexts.

Apart from that, the affiliative and proximity indexes do not correlate with each other, which implies that social relationships are much more complex and the index needs to be further improved. As mentioned above, the implementation of spacing behaviour, not only lying in proximity, could possibly provide a better correlation of affiliative behaviour and proximity.

4.4.*Effects on social associations*

The numbers of pigs in a pen mainly influenced the percentage and strength of associations that pigs have formed between each other. The more pigs were kept in a pen, the lower was the percentage of weak and strong associations that pigs developed. This suggests that pigs can easier build positive social relationships, when there is a smaller number of pen mates. This would mostly fit to their natural behaviour in wild boars, which live in groups consisting of two to four related, mature sows and their offspring (Graves, 1984; Meynhardt, 1982). However, the way the index was calculated, this result needs to be seen with caution. The indexes were divided by numbers of pigs in a group, which may have created a bias by favouring pigs in small groups and disfavouring pigs in large groups, at equivalent occurrences of behaviours.

Gender did also influence social bonds. Before weaning, males tended to have fewer weak associations than females, whereas there was no gender difference in the percentage of strong associations. After weaning, this was contrary with males having significantly more weak associations than females. The strongest associations were also higher in males suggesting that males make fewer but stronger associations than females. In their natural environment wild adult male boars typically lead a solitary life, while the sows stay with closely related other females and litters in stable groups (Gonyou, 2001). This is in line with the results of our study where more strong associations were observed in females than in males.

Fostered piglets tended to have fewer weak associations before weaning, which seems quite reasonable as they can be integrated up to 72 hours postpartum into the new group. In the first days fostered piglets spend less time with the litter and often try to escape (Horrell, 1982). Fostered piglets usually do not acoustically converge with their new littermates until after three weeks (Špinka et al., 2019), which might complicate the integration in the group. However, this trend did not continue after weaning and seems not to affect the social associations being made thereafter. This emphasizes the ability of pigs for social adaptation.

Body weight of the piglets did not affect their social associations. In some primates species, body weight can be important for calculating social bonds, as there is an association between bonds and the mostly heavier alpha male (Drake et al., 2000). However, according to our findings, differences in body weight did not influence affiliative behaviour in pigs.

4.5.*Implications on animal welfare*

Based on affiliative behaviour and proximity, pigs appear to form social bonds. Therefore regrouping of pigs, which is common in conventionally farming, may disrupt those bonds. This can result in increased aggression and can lead to a major welfare issue (Arey & Edwards, 1998). Having a familiar partner in a stressful situation can improve the ability to cope with stress (Kanitz et al., 2014), thus social bonds can be an important factor to improve pig welfare.

On that basis the application of fostering of piglets should be considered carefully. In their first weeks of life piglets are more vulnerable to stress (Kanitz et al., 2014) and as shown within this study fostered piglets seem to be less capable of forming strong social bonds before weaning. The lack of strong social bonds may impose additional difficulties for fostered piglets, which are already exposed to many stressors and physiological challenges when entering a different litter (for example, facing aggression, competing for a place at the udder, and a different pathogen load). This research therefore encourages the current recommendations in practice to foster piglets; for example in at least a pair so that at least two siblings will remain together in the new environment.

5. Conclusion

Affiliative behaviours, like nose-to-nose contact, grooming, lying in proximity and other affiliation, appears very frequently in the total behavioural repertoire of pigs. Therefore, they seem to be good indicators that should be used when considering social bonds. As pointed out in several studies with different species, a combination of different social behaviours could be used to calculate a sociality index. The lack of a correlation between affiliative behaviour and proximity in pigs does need to be confirmed in broader settings to investigate whether a composite sociality index can be meaningful in pigs. The strength of associations that pigs have formed can be influenced by the numbers of pigs in a pen, also gender differences are noticeable. We encourage further research in applying the sociality index in pigs, to gain comparative values and to deepen the understanding of social relationships in this species.

6. Abstract

Social relationships, of which social bonds are one aspect, play an important role in many social living species. However, positive social relationships in pigs have been hardly studied so far. The aim of this study was to record affiliative behaviours and spatial proximity while lying to assess whether their integration in a composite sociality index (CSI) reflects a putative social bond. Spatial proximity and affiliative behaviours, like nose-to-nose contact, allo-grooming and other affiliative behaviours were recorded by live behavioural observations from 285 piglets for three weeks prior to weaning and the CSI was calculated. At weaning, 132 pigs were relocated in different weaning pens. Observations continued at week four and week seven and CSI were again calculated. Affiliative behaviour occurred on average in 9.66 ± 0.212 % (range 0 – 63%) of the total observations. Pigs were lying in 91.8% of the observations in proximity in body contact to one another. Applying the CSI, 90% of the piglets formed social bonds of varying strengths. However, the CSI in the week after weaning was only weakly correlated with the CSI in week seven, implying that social relationships in pigs change over time. Still, the sociality index needs to be further improved, as the index of affiliative behaviour did not correlate significantly with the index of proximity at most time points.

7. Zusammenfassung

Soziale Beziehungen, von denen soziale Bindungen ein Aspekt sind, spielen bei vielen sozialen Lebewesen eine wichtige Rolle. Positive soziale Beziehungen bei Schweinen wurden bisher jedoch kaum untersucht. Ziel dieser Studie war es, affiliatives Verhalten und räumliche Nähe während des Liegens aufzuzeichnen und zu bewerten, ob ihre Integration in einem zusammengesetzten Sozialitätsindex eine mutmaßliche soziale Bindung widerspiegelt. Die räumliche Nähe und affiliatives Verhalten, wie Nase-zu-Nase Kontakt, soziale Körperpflege oder andere Affliation, wurden drei Wochen vor dem Absetzen durch Verhaltensbeobachtungen von 285 Ferkeln aufgezeichnet und ein Sozialitätsindex wurde berechnet. Beim Absetzen wurden 132 Schweine in verschiedene Entwöhnungsställe umgesiedelt. Die Beobachtungen wurden in Woche vier und Woche sieben fortgesetzt, und der Sozialitätsindex wurde erneut berechnet. Das affliative Verhalten betrug im Durchschnitt 9,66 ± 0,212% (Bereich 0 - 63%) der Gesamtbeobachtungen. In 91,8% der Beobachtungen lagen Schweine im Körperkontakt zueinander. Unter Anwendung des Sozialitätsindex bildeten 90% der Ferkel soziale Bindungen unterschiedlicher Stärke. Der Sozialitätsindex in der Woche nach dem Absetzen korrelierte jedoch nur schwach mit dem Sozialitätsindex in Woche sieben, das impliziert, dass sich die Beziehungen bei Schweinen im Laufe der Zeit ändern. Dennoch sollte der Sozialitätsindex weiter verbessert werden, da der Index des affiliativen Verhaltens an den meisten Zeitpunkten nicht signifikant mit dem Index der Nähe korrelierte.

8. References

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

Armitage, K. B., & Schwartz, O. A. (2000). Social enhancement of fitness in yellow-bellied marmots. *Proceedings of the National Academy of Sciences*, *97*(22), 12149–12152. https://doi.org/10.1073/pnas.200196097

Arnold, G. W., Wallace, S. R., & Rea, W. A. (1981). Associations between individuals and home-range behaviour in natural flocks of three breeds of domestic sheep. *Applied Animal Ethology*, *7*(3), 239–257. https://doi.org/10.1016/0304-3762(81)90081-X

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*(3), 375–397. https://doi.org/10.1016/j.physbeh.2007.02.003

Bracke, M. B. M. (2011). Review of wallowing in pigs: Description of the behaviour and its motivational basis. *Applied Animal Behaviour Science*, *132*(1–2), 1–13. https://doi.org/10.1016/j.applanim.2011.01.002

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. https://doi.org/10.1016/j.applanim.2013.02.008

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*(33), 13850–13853. https://doi.org/10.1073/pnas.0900639106

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

Carpenter, C. R. (1965). Naturalistic Behavior of Nonhuman Primates. C. R. Carpenter. Pennsylvania State University Press, University Park, 1964. X + 454 pp. Illus. $9.50. *Science*, *148*(3671), 827–827. https://doi.org/10.1126/science.148.3671.827-a

Colvin, J., & Tissier, G. (1985). Affiliation and reciprocity in sibling and peer relationships among free-ranging immature male rhesus monkeys. *Animal Behaviour*, *33*(3), 959–977. https://doi.org/10.1016/S0003-3472(85)80030-0

Cords, M. (1997). Friendships, alliances, reciprocity and repair. In A. Whiten & R. W. Byrne (Eds.), *Machiavellian Intelligence II* (1st ed., pp. 24–49). Cambridge University Press. https://doi.org/10.1017/CBO9780511525636.003

Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Social stressors and coping mechanisms in wild female baboons (Papio hamadryas ursinus). *Hormones and Behavior*, *53*(1), 254–265. https://doi.org/10.1016/j.yhbeh.2007.10.007

Drake, M., Grant, K. A., Prioleau, O. A., Nader, S. H., Kaplan, J. R., & Nader, M. A. (2000). Predictors of social status in cynomolgus monkeys (Macaca fascicularis) after group formation. *American Journal of Primatology*, *52*(3), 115–131.

Durrell, J. L., Sneddon, I. A., O'Connell, N. E., & Whitehead, H. (2004). Do pigs form preferential associations? *Applied Animal Behaviour Science*, *89*(1–2), 41–52. https://doi.org/10.1016/j.applanim.2004.05.003

Erhard, H. W., Mendl, M., & Ashley, D. D. (1997). Individual aggressiveness of pigs can be measured and used to reduce aggression after mixing. *Applied Animal Behaviour Science*, *54*(2–3), 137–151. https://doi.org/10.1016/S0168-1591(97)00068-3

Fairbanks, L. A. (1980). Relationships among adult females in captive vervet monkeys: Testing a model of rank-related attractiveness. *Animal Behaviour*, *28*(3), 853–859. https://doi.org/10.1016/S0003-3472(80)80145-X

Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H., & Hammerschmidt, K. (2017). Quantifying social complexity. *Animal Behaviour*, *130*, 57–66. https://doi.org/10.1016/j.anbehav.2017.06.003

Fraser, D. (1978). Observations on the behavioural development of suckling and early-weaned piglets during the first six weeks after birth. *Animal Behaviour*, *26*, 22–30. https://doi.org/10.1016/0003-3472(78)90004-0

Gonyou, H. W. (2001). The social behaviour of pigs. In *Social behaviour in farm animals* (pp. 147–176). CABI Publishing.

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. https://doi.org/10.1016/j.applanim.2020.105045

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

Gygax, L., Neisen, G., & Wechsler, B. (2010). Socio-Spatial Relationships in Dairy Cows: Socio-Spatial Relationships in Dairy Cows. *Ethology*, *116*(1), 10–23. https://doi.org/10.1111/j.1439-0310.2009.01708.x

Haunhorst, C. B., Heesen, M., Ostner, J., & Schülke, O. (2017). Social bonds with males lower the costs of competition for wild female Assamese macaques. *Animal Behaviour*, *125*, 51–60. https://doi.org/10.1016/j.anbehav.2017.01.008

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, *11*(1), 1. https://doi.org/10.2307/2800384

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

Horrell, R. I. (1982). Immediate behavioural consequences of fostering 1-week-old piglets. *The Journal of Agricultural Science*, *99*(2), 329–336. https://doi.org/10.1017/S0021859600030100

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 behaviour of growing pigs in response to high temperature and humidity. *Applied Animal Behaviour Science*, *91*(1–2), 1–16. https://doi.org/10.1016/j.applanim.2004.10.020

Jensen, P., Stangel, G., & Algers, B. (1991). Nursing and suckling behaviour of semi-naturally kept pigs during the first 10 days postpartum. *Applied Animal Behaviour Science*, *31*(3–4), 195–209. https://doi.org/10.1016/0168-1591(91)90005-I

Kanitz, E., Hameister, T., Tuchscherer, M., Tuchscherer, A., & Puppe, B. (2014). Social support attenuates the adverse consequences of social deprivation stress in domestic piglets. *Hormones and Behavior*, *65*(3), 203–210. https://doi.org/10.1016/j.yhbeh.2014.01.007

Lindburg, D. G. (1973). Grooming behavior as a regulator of social interactions in rhesus monkeys. In C. R. Carpenter (Ed.), *Behavioral Regulators of Behavior in Primates* (pp. 124–148). Bucknell University Press.

Lonsdorf, E. V., Anderson, K. E., Stanton, M. A., Shender, M., Heintz, M. R., Goodall, J., & Murray, C. M. (2014). Boys will be boys: Sex differences in wild infant chimpanzee social interactions. *Animal Behaviour*, *88*, 79–83. https://doi.org/10.1016/j.anbehav.2013.11.015

Manning, A., & Dawkins, M. S. (2012). *An Introduction to Animal Behaviour* (Sixth ed.). Cambridge University Press.

Massen, J., Sterck, E., & de Vos, H. (2010). Close social associations in animals and humans: Functions and mechanisms of friendship. *Behaviour*, *147*(11), 1379–1412. https://doi.org/10.1163/000579510X528224

McBride, G. (1971). Theories of Animal Spacing: The Role of Flight, Fight and Social Distance. In A. H. Esser (Ed.), *Behavior and Environment* (pp. 53–68). Springer US. https://doi.org/10.1007/978-1-4684-1893-4_6

McCort, W. D., & Graves, H. B. (1982). Social dominance relationships and spacing behavior of swine. *Behavioural Processes*, *7*(2), 169–178. https://doi.org/10.1016/0376-6357(82)90025-0

McFarland, R., Murphy, D., Lusseau, D., Henzi, S. P., Parker, J. L., Pollet, T. V., & Barrett, L. (2017). The 'strength of weak ties' among female baboons: Fitness-related benefits of social bonds. *Animal Behaviour*, *126*, 101–106. https://doi.org/10.1016/j.anbehav.2017.02.002

Meese, G. B., & Ewbank, R. (1973). The establishment and nature of the dominance hierarchy in the domesticated pig. *Animal Behaviour*, *21*(2), 326–334. https://doi.org/10.1016/S0003-3472(73)80074-0

Meynhardt, H. (1982). *Schwarzwildreport. Mein Leben unter Wildschweinen*. Neumann-Neudamm.

Muns, R., Nuntapaitoon, M., & Tummaruk, P. (2016). Non-infectious causes of pre-weaning mortality in piglets. *Livestock Science*, *184*, 46–57. https://doi.org/10.1016/j.livsci.2015.11.025

Newberry, R. C., & Wood-Gush, D. G. M. (1986). Social relationships of piglets in a semi-natural environment. *Animal Behaviour*, *34*(5), 1311–1318. https://doi.org/10.1016/S0003-3472(86)80202-0

Newberry, R., & Swanson, J. (2001). Breaking social bonds. In L. J. Keeling & H. W.

Gonyou (Eds.), *Social behaviour in farm animals* (pp. 307–331). CABI. https://doi.org/10.1079/9780851993973.0307

Newton-Fisher, N. E., & Lee, P. C. (2011). Grooming reciprocity in wild male chimpanzees. *Animal Behaviour*, *81*(2), 439–446. https://doi.org/10.1016/j.anbehav.2010.11.015

Olczak, K., Nowicki, J., & Klocek, C. (2015). Pig behaviour in relation to weather conditions – a review. *Annals of Animal Science*, *15*(3), 601–610. https://doi.org/10.1515/aoas-2015-0024

Pearce, E., Wlodarski, R., Machin, A., & Dunbar, R. I. M. (2017). Variation in the β-endorphin, oxytocin, and dopamine receptor genes is associated with different dimensions of human sociality. *Proceedings of the National Academy of Sciences*, *114*(20), 5300–5305. https://doi.org/10.1073/pnas.1700712114

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

Petersen, V. (1994). The development of feeding and investigatory behaviour in free-ranging domestic pigs during their first 18 weeks of life. *Applied Animal Behaviour Science*, *42*(2), 87–98. https://doi.org/10.1016/0168-1591(94)90149-X

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

Portele, Scheck, Siegmann, Feitsch, Maschat, Rault, & Camerlink. (2019). Sow-Piglet Nose Contacts in Free-Farrowing Pens. *Animals*, *9*(8), 513. https://doi.org/10.3390/ani9080513

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social Bonds Enhance Reproductive Success in Male Macaques. *Current Biology*, *20*(24), 2207–2210. https://doi.org/10.1016/j.cub.2010.10.058

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. *Behavioral Ecology and Sociobiology*, *61*(2), 183–195. https://doi.org/10.1007/s00265-006-0249-2

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*(15), 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067

Smith, K. P., & Christakis, N. A. (2008). Social Networks and Health. *Annual Review of Sociology*, *34*(1), 405–429. https://doi.org/10.1146/annurev.soc.34.040507.134601

Špinka, M., Syrová, M., Policht, R., & Linhart, P. (2019). Early vocal ontogeny in a polytocous mammal: No evidence of social learning among sibling piglets, Sus scrofa. *Animal Behaviour*, *151*, 9–19. https://doi.org/10.1016/j.anbehav.2019.02.018

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. https://doi.org/10.1016/0168-1591(91)90006-J

Stookey, J. M., & Gonyou, H. W. (1994). The effects of regrouping on behavioral and production parameters in finishing swine1. *Journal of Animal Science*, *72*(11), 2804–2811. https://doi.org/10.2527/1994.72112804x

Turner, S. P., Horgan, G. W., & Edwards, S. A. (2003). Assessment of sub-grouping behaviour in pigs housed at different group sizes. *Applied Animal Behaviour Science*, *83*(4), 291–302. https://doi.org/10.1016/S0168-1591(03)00139-4

Turner, S. P., Nath, M., Horgan, G. W., & Edwards, S. A. (2013). Measuring chronic social tension in groups of growing pigs using inter-individual distances. *Applied Animal Behaviour Science*, *146*(1–4), 26–36. https://doi.org/10.1016/j.applanim.2013.03.012

Val-Laillet, D., Guesdon, V., von Keyserlingk, M. A. G., de Passillé, A. M., & Rushen, J. (2009). Allogrooming in cattle: Relationships between social preferences, feeding displacements and social dominance. *Applied Animal Behaviour Science*, *116*(2–4), 141–149. https://doi.org/10.1016/j.applanim.2008.08.005

Wasilewski, A. (2003). *'Freundschaft' bei Huftieren? - Soziopositive Beziehungen zwischen nicht-verwandten artgleichen Herdenmitgliedern* [Application/pdf]. https://doi.org/10.17192/Z2003.0639

Watts, D. P. (1994). Social relationships of immigrant and resident female mountain gorillas, II: Relatedness, residence, and relationships between females. *American Journal of Primatology*, *32*(1), 13–30. https://doi.org/10.1002/ajp.1350320103

Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L.

(2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior*, *54*(1), 170–177. https://doi.org/10.1016/j.yhbeh.2008.02.009

Wolter, R., Stefanski, V., & Krueger, K. (2018). Parameters for the Analysis of Social Bonds in Horses. *Animals*, *8*(11), 191. https://doi.org/10.3390/ani8110191

Yang, Y. C., Boen, C., Gerken, K., Li, T., Schorpp, K., & Harris, K. M. (2016). Social relationships and physiological determinants of longevity across the human life span. *Proceedings of the National Academy of Sciences*, *113*(3), 578–583. https://doi.org/10.1073/pnas.1511085112