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Social network analysis in free-ranging Kune Kune pigs (*Sus scrofa domesticus*) – tolerated co-feeding according to their social relationships

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## Abstract

Social animals living in groups interact with each other on a regular basis and can therefore form complex relationships. These interactions do not only affect the type of relationships between these animals but could also positively affect the individual's fitness because the individual might benefit from increased foraging efficiency or an increased reproductive success. Interactions among members of the social group that follow regularities or patterns can be illustrated on the basis of a social network analysis. Social networks have been described in different animal species, for example in fish like guppies, in birds like jackdaws or in mammals like wild boars.

This study aimed to investigate the social interaction patterns of a group of 41 free-ranging domestic Kune Kune pigs (*Sus scrofa domesticus*), which consisted of three sows and their litters. The social network analysis focused on (I) finding differences between three matriline families, each consisting of a sow and her litters, (II) investigating the effect of age on social interactions between the three age classes, mother-sows born in 2013 and their litters born in 2014 and in 2015 and (III) evaluating relationships between all pigs to detect specific relationship types (affiliative and agonistic). The relationships types found in the social network analysis were then tested in an artificial setting (tolerated co-feeding tests) in order to provide empirical evidence of whether social network data taken through regular observations will provide the same insight into a social group than a behavioral experiment would do.

Social network analysis revealed that the main difference with regard to both the frequency and the type of social interaction rather lies between the mother-sows and their litters, than between the two age classes of the litters. Comparisons between the three families revealed that pigs of the Z-family showed more socionegative behaviors towards others than pigs of the R-family. There was clear evidence for a variation of relationship types, namely affiliative, agonistic and neutral relationship types were found.

Tolerated co-feeding tests revealed that, in contrast to the natural setting, there were no significant differences with regard to feeding- and proximity-related or sociopositive and socionegative interactions between dyads with an affiliative relationship and dyads with an agonistic relationship. Interestingly, these behavioral tests failed to mirror the relationships found in the observations of natural behavior. Forced feeding competition seems to uncover only a small part of the multi-faceted relationship between these pigs, mainly the dominance relationship.

## **Zusammenfassung**

Gesellig lebende Tiere interagieren miteinander und können komplexe Beziehungen formen. Diese Interaktionen beeinflussen nicht nur die Art der Beziehungen, sondern können sich auch positiv auf das Überleben der Tiere auswirken, wenn ein Individuum von der gesteigerten Effizienz bei der Nahrungsaufnahme oder von erhöhtem Fortpflanzungserfolg profitiert. Regelmäßigkeiten oder Interaktionsmuster zwischen den Mitgliedern einer sozialen Gruppe darzustellen, ermöglicht die soziale Netzwerkanalyse. Soziale Netzwerke wurden bereits bei zahlreichen Tierarten beschrieben, zum Beispiel bei Fischen wie Guppies, Vögeln wie Dohlen oder bei Säugetieren wie Wildschweinen.

Diese Studie hatte das Ziel die sozialen Interaktionsmuster einer Gruppe von 41 Kune Kune Schweinen (*Sus scrofa domesticus*), welche aus drei Sauen und ihren Würfen bestand, zu analysieren. Die soziale Netzwerkanalyse war fokussiert auf (I) Unterschiede zwischen den drei Familien zu finden, (II) den Effekt von Alter auf soziale Interaktionen zwischen den drei Altersklassen, den drei im Jahr 2013 geborenen Sauen und ihren in den Jahren 2014 und 2015 geborenen Würfen zu untersuchen und (III) Beziehungen zwischen den Schweinen zu evaluieren, um Dyaden mit besonders freundlichen und solche mit besonders feindlichen Beziehungen auszuwählen. Die Beziehungen, welche in semi-natürlichen Bedingungen in der sozialen Netzwerkanalyse gefunden wurden, wurden anschließend unter künstlichen Bedingungen (in co-feeding-Tests) getestet, um Hinweise zu finden ob soziale Netzwerkdaten welche durch regelmäßige Beobachtungen aufgenommen wurden, dieselbe Einsicht in soziale Gruppen liefern wie Verhaltensexperimente.

Die soziale Netzwerkanalyse hat gezeigt, dass der Hauptunterschied im Bezug auf die Frequenz aber auch die Art der sozialen Interaktionen nicht zwischen den beiden Altersklassen der Würfe liegt sondern zwischen den Muttersauen und ihren Würfen. Der Vergleich zwischen den drei Familien hat gezeigt, dass Schweine aus der Z-Familie mehr sozionegatives Verhalten gegenüber anderen Schweinen zeigen als Schweine aus der R-Familie.

Es gab deutliche Hinweise für Variationen in der Qualität der Beziehungen der Tiere untereinander, da sowohl freundschaftliche, feindliche als auch neutrale Beziehungen gefunden wurden.

In den co-feeding-Tests hat sich gezeigt, dass es, im Gegensatz zu den natürlichen Bedingungen, keine signifikanten Unterschiede zwischen Dyaden mit einer affiliativen und Dyaden mit einer agonistischen Beziehung in Bezug auf Fressverhalten, Näheverhalten, soziopositives und sozionegatives Verhalten gibt. Interessanterweise, konnten die

Verhaltensexperimente nicht die Beziehung der Tiere, welche in den Verhaltensbeobachtungen gefunden wurden, widerspiegeln. Erzwungener Wettbewerb um Futter scheint nur einen kleinen Teil der facettenreichen Beziehungen zwischen diesen Schweinen aufzudecken, hauptsächlich Dominanzbeziehungen.

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## 1. Introduction

Social animals living in groups interact with each other on a regular basis and can therefore form complex relationships. These interactions and the type of the relationships could positively affect the individual's fitness (Wey et al., 2008) because the individual might benefit from increased foraging efficiency as conspecifics might help each other to locate food sources. Other advantages could be an increased feeding time due to benefiting of group member's vigilance or a diluting effect of the group when it comes to predation (Shettleworth, 2010). But the individual could also increase its reproductive success if possible mating partners are around in the group or if group members help to raise the offspring (Rubenstein, 1978).

A commonly used method to describe the style and structure of social groups are verbal descriptions. An alternative provides social network analysis (Macdonald & Voelkl, 2015), which enables us to describe social groups as regularities or patterns of interactions among members of the social group (Wassermann & Faust, 1994). In all animal (and also human) groups that have been investigated, evidence for social interaction patterns that strongly differ from randomness have been found (i.e. individuals do have a greater affinity to interact with certain individuals). Furthermore, individual differences in social contact patterns have been found, indicating that some individuals are in contact with many conspecifics while others are in contact with few conspecifics, which is measured by *centrality* (Krause & Ruxton, 2002).

A social network is usually displayed by using *nodes*, representing individuals that are connected by *edges*, representing the detected social interactions between them. The strength of these social interactions can be displayed by the thickness of the edges, which is commonly described as 'weighted'. Furthermore, as interactions can be directed from one individual to another, edges can also be displayed as *arrows*, thereby indicating sender and receiver (Krause et al., 2007).

As there are different contexts in which social networks can be described, for example the transmission of diseases or information, kinship connection, sharing of resources or dominance hierarchies, there are different types of measures to describe social networks. Individuals' positions within the network can be described with individual measures, such as *node degree* (number of conspecifics a focal animal interacts with), *outdegree* (number of interactions with conspecifics initiated by a focal animal) or *centrality* (measure of the number and strength of edges that also considers the centrality of the individuals that are connected to the individual in focus). The composition of social networks, on the other hand, can be described by group measures, such as *density* (number of actual edges divided by the



number of possible edges), *average path length* (average of all path lengths between all pairs of nodes when path length is defined as the lowest number of edges between two nodes) and *diameter* (longest path in the network). To describe if there are subgroups in a network intermediate measures are used, such as *clustering coefficient* (number of actual edges between neighbors divided by the maximal number of possible edges between them) and *cliquishness* (how much division into subgroups there is within a group) (Wey et al., 2008). In this study, we focus on the individual measure *centrality* as it considers the weights on the edges, i.e. frequency of interactions, and the direction of interactions. Furthermore, the non-local neighborhood is included in the measurement, i.e. not only how many neighbors a pig has but also how many neighbors its neighbors have (Müller et al., 1999; Jordán et al., 2003). There are different types of social interactions, for instance sociopositive or socionegative interactions, for each of which social networks can be created. These networks show who is connected to whom and which type of relationship individuals have with each other. Yerkes & Yerkes (1935) claimed that the type of interactions between two animals is crucial for the nature of the relationship these individuals do have with each other. A lot of socionegative interactions and only a few if any sociopositive interactions would result in an agonistic relationship while an affiliative relationship would consist of mainly sociopositive and only few socionegative interactions.

Sociopositive interactions indicate an affiliative relationship if being regularly shown, such as tolerance for (close) proximity or forms of gentle body contact like grooming, touching or embracing (Massen et al., 2010).

Studies that investigated different types of relationships found that for example female feral goats (*Capra hircus*) prefer the proximity of certain individuals to the proximity of other individuals. These affiliative social bonds were consistent and actively maintained by both partners (Stanley & Dunbar, 2013). Schwab et al. (2008) showed in common ravens (*Corvus corax*) that siblings sat longer close to each other and spent more time in close proximity to each other compared to non-siblings. Furthermore, they could show that objects were handled together by siblings more often than by non-siblings and a sibling that handled an object was approached more frequent than a non-sibling who handled an object. Reinhardt & Reinhardt (1983) found in cattle (*Bos indicus*) that mother cows and their daughters prefer the proximity of each other to the proximity of non-related conspecifics, even when the daughters themselves have had calves already. Furthermore, cows engaged more in social licking with their own calves compared to non-related calves.

Loretto et al. (2012) showed that common ravens tolerate non-kin less than kin and low-intensity aggression was more frequent between non-kin than between kin. In red grouse (*Lagopus lagopus scoticus*) it has been found that agonistic encounters between non-kin neighbors occurred more frequently than between kin neighbors (Watson et al., 1994).

In addition to the species mentioned above, social networks have been described in different vertebrate species. For example in fish like guppies (*Poecilia reticulata*) (Croft et al., 2004) and three-spined sticklebacks (*Gasterosteus aculeatus*) (Ward et al. 2002), in reptiles like sleepy lizards (*Tiliqua rugosa*) (Leu et al., 2010), in birds like great tits (*Parus major*) (Farine & Sheldon, 2015) and jackdaws (*Corvus monedula*) (Kubitza et al. 2015) and in mammals like rhesus monkeys (*Macaca mulatta*) (Corr, 2011), in cetaceans like bottlenose dolphins (*Tursiops truncatus*) (Lusseau, 2003) and in ungulates like African buffalos (*Syncerus caffer*) (Cross et al., 2004).

Podgorski et al. (2014) investigated the social structure of wild boars (*Sus scrofa*) and found that the association and interaction pattern of wild boars is not coincidental, which means that wild boars prefer the interaction with certain conspecifics to the interaction with other conspecifics. Furthermore, Podgorski et al. (2014) showed that females within a social unit have a higher degree of relatedness than individuals of different social units. This could lead to increased survival of the offspring, because females help to raise the offspring of other related females which in turn could positively affect the fitness of the females (inclusive fitness). In contrast, males did not show the same preferences like females; males showed preferences for associations with unrelated males.

Domestic pigs (*Sus scrofa domesticus*) are a highly sociable species (Gonyou, 2011) that has descended from a variety of wild boar sub species (Giuffra et al., 2000) and is now living in human care, mainly for the purpose of food production, but sometimes also as study subjects for various medical procedures (Pond & Houpt, 1978). The housing conditions can vary drastically, but only seldomly take into account the social nature and natural group composition of these animals.

Even though there is a significant amount of research devoted to medical and production enhancing questions regarding domestic pigs, the lack of knowledge about their social lives under natural or semi-natural conditions makes them an interesting model species for social network analysis. Stolba & Wood-Gush (1989), as one of the very few researchers, observed the behavior of more than 13 different groups of domestic pigs in a semi-natural enclosure over a period of more than three years. The groups consisted of adult, sub-adult and juvenile pigs of both sexes. They found that pigs live in matriline sounders, which consist of related

mothers and their recent litters and juvenile offspring of previous litters (Stolba & Wood-Gush, 1989). Males of seven to eight month of age disperse and live on the edges of these groups and only interact with females during breeding season (Graves, 1984). Within these sounders, sociopositive behaviors like mutual sniffing, touching or grouping are frequently shown. Socionegative behaviors like fighting are relatively rare (Stolba & Wood-Gush, 1989), as pigs establish dominance hierarchies that are based on the results of bidirectional agonistic interactions (Puppe & Tuchscherer, 1994). The animals have to learn to behave in an adequate manner according to the behavior of their group members which is important for the stability of the group, the reduction of stressful social encounters and in order to access resources (Arey & Franklin, 1995). But also heat of sows influences social encounters of pigs. When sows are in heat, a condition that lasts for about three days and occurs every 18 to 24 days, they are seeking the proximity of boars, stand still in reaction to a boar's stimulation and allow the boar to mount and copulate. Furthermore, sows in heat show more touching of the flanks of other individuals and mounting behavior. But at the end of the heat the sow's toleration of the boar decreases and the sow behaves increasingly aggressive towards the boar. Like many group living animals, pigs also show synchronization of behavior, feeding or resting (Spinka, 2002). In order to do so, they have to pay a high amount of attention to actions of their group members and especially to certain members of the group (Stolba & Wood-Gush, 1989). Evidence has been found that pigs have preferences with regard to social interactions, which means that they interact more with certain conspecifics than with others (Newberry & Wood-Gush, 1986). Pigs that are familiar with each other greet each other with contact grunts and naso-nasal contact. To avoid aggressive interactions with conspecifics, pigs tend to distribute during foraging, given that they have the possibility to do so. It has been shown that pigs tend to form subgroups depending on their age. Subgroups can consist of adult animals, sub-adults or juvenile individuals (Stolba & Wood-Gush, 1989) and within the juveniles littermates tend to spend more time together (Newberry & Wood-Gush, 1986). Both Podgorski et al. (2014) and Stolba & Wood-Gush (1989) observed pigs in natural or semi-natural environments. However, they didn't conduct behavioral tests to see if the relationships uncovered by their observations could be confirmed by specific, experimentally controlled tests. The type of relationship individuals do have with each other influences the occurrence of co-feeding, as Yerkes & Yerkes (1935) observed in monkeys that there has to be a friendly relationship between the donor and the recipient in order for food sharing to occur. Between individuals with an agonistic relationship food sharing was never observed.

In general, two forms of food sharing can be distinguished. The first one describes offering food to another individual with the hand, mouth or beak (Kasper et al., 2008). The second form of food sharing describes tolerated co-feeding, which means feeding together at a food source that could be monopolized (Scheid et al., 2008). Animals may share food to gain immediate or delayed fitness benefits like receiving food, grooming, sex or support in conflicts (Brosnan & DeWaal, 2002; Stevens, 2004). Food sharing does not only occur between related animals, like parents and their offspring, but also between unrelated animals, like mating partners. Among related individuals the costs for the animal which shares food can be explained with kin selection (Hamilton, 1964), whereas the “food-for-sex hypothesis” can serve as an explanation for food sharing between males and females. This hypothesis states that males share food with sexually receptive females to increase their chance to mate with them (Kaplan & Hill, 1985).

Food sharing may also occur for the purpose of harassment avoidance, which means that the costs for giving up a resource are lower than keeping and defending it (Gilby, 2006). Depending on the context (at specific time points or with a specific partner) rejecting harassment could cause different social costs for an individual, for example not sharing food with “friends” or mating partners could result in the loss of reciprocal benefits in the future (Jaeggi & van Schaik, 2011).

The aim of this study was to investigate the social interaction patterns of 41 free-ranging domestic Kune Kune pigs (*Sus scrofa domesticus*). Furthermore, it was tested whether specific relationship types of agonistic and affiliative nature that were found in the social network also persist in an artificial setting, the tolerated co-feeding tests. This was done in order to provide empirical evidence of whether social network data taken through regular observations will provide the same insight into a social group than a behavioral experiment would do.

We predicted that there are social networks that differ from randomness, i.e. some animals do have many interactions while others have less. Furthermore, we expected that there are differences in social interactions with regard to family or age class of the individuals like more social interactions of the litters born in 2015 compared to the litters born in 2014 or the mother-sows, as juveniles might be more active. The different activity patterns of adult mother-sows and their juvenile litters might influence with whom they interact but also how often they interact with each other, as the less active mother-sows might rest for example while the litters are foraging on the meadow and interact with littermates.

We expected that not only in semi-natural conditions but also in the artificial test setting socionegative behaviors will occur more often in dyads with an agonistic relationship, whereas sociopositive behaviors were predicted to occur more often in dyads with an affiliative relationship. Dyads with an affiliative relationship were expected to stay closer to each other while feeding than dyads with agonistic relationships would do and show more co-feeding behavior.

A possible alternative to our predictions could be that the behavior of pigs in co-feeding tests is more influenced by the dominance hierarchy and less by the type of relationship the pigs have, especially when it comes to competition for a highly attractive food reward. We know that pigs establish a dominance hierarchy, which influences, among others, access to valuable resources.

## 2. Methods

### 2.1. Study subjects

Altogether, the social network of 41 Kune Kune pigs (*Sus scrofa domesticus*), 22 females and 19 males, was investigated (Table 1). Three gilts from 2013, raised in Pichl bei Wels, were brought to the Haidlhof Research Station close to Bad Vöslau, Lower Austria, in 2014, when all of them were already pregnant. In the same year, 18 piglets were born and raised, followed by a second group of 20 piglets in 2015, after a boar had been brought in for breeding only. To avoid inbreeding the male offspring have been made infertile at the age of five months by vasectomy, not by castration, so that they are able to develop their natural behavior as boars and take their natural position in the sounder structure.

The pigs are kept on an 8 ha pasture that is used in a rotational grazing system, i.e. the pasture that contains a good mixture of clover and grass is divided into three parts that are rotated each year to avoid hygienic problems and always offer fresh food to the pigs. The enclosure comprises a forest area where six well-insulated A-shaped huts offer shelter for the pigs during the night or in cold weather conditions. The animals have *ad libitum* access to the pasture and to water and are provided with a water-pit for bathing. They are additionally fed once a day with a varying mixture of fruits, vegetables, corn and bread.

**Table 1. List of all observed pigs.** Each column represents one family (the first pig is the mother-sow of all the other pigs in the same column). Names, abbreviations, age and sex are listed. Age class (1) indicates born in 2013, age class (2) indicates born in 2014 and age class (3) indicates born in 2015. Males are shown in bold type face.

Abbreviations (and age class)	Names	Abbreviations (and age class)	Names	Abbreviations (and age class)	Names
B0 (1)	Beauty	R0 (1)	Rosalie	Z0 (1)	Zora
B1 (2)	Bella	R1 (2)	Rapunzel	<b>Z1 (2)</b>	<b>Zacharias</b>
<b>B2 (2)</b>	<b>Benjamin</b>	<b>R2 (2)</b>	<b>Rasputin</b>	Z2 (2)	Zafira
B3 (2)	Bessy	<b>R3 (2)</b>	<b>Romeo</b>	<b>Z3 (2)</b>	<b>Zampano</b>
B4 (2)	Bibi	R4 (2)	Ronja	<b>Z4 (2)</b>	<b>Zazou</b>
B5 (2)	Bijou	<b>R5 (2)</b>	<b>Rudi</b>	<b>Z5 (2)</b>	<b>Zerberus</b>
B6 (2)	Blume	R6 (3)	Radieschen	Z6 (2)	Zoe
<b>B7 (3)</b>	<b>Baldur</b>	<b>R7 (3)</b>	<b>Radomir</b>	Z7 (2)	Zwetschge
<b>B8 (3)</b>	<b>Barbarossa</b>	R8 (3)	Raya	<b>Z8 (3)</b>	<b>Zafran</b>
B9 (3)	Belana	<b>R9 (3)</b>	<b>Ronon</b>	<b>Z9 (3)</b>	<b>Zardoz</b>
B10 (3)	Bernadette	R10 (3)	Rosine	<b>Z10 (3)</b>	<b>Zeppelin</b>
B11 (3)	Blossom	R11 (3)	Rubina	<b>Z11 (3)</b>	<b>Zeus</b>
<b>B12 (3)</b>	<b>Bolero</b>			Z12 (3)	Zirbe
<b>B13 (3)</b>	<b>Bruno</b>			Z13 (3)	Zita
				<b>Z14 (3)</b>	<b>Zoltan</b>

## 2.2. Social network analysis

### 2.2.1. Preparation phase

Before the observation period started, a two weeks habituation phase took place, to get familiar with the behavioral repertoire of domestic pigs and recognize the individuals safely, followed by the preparation of an ethogram (Table 2). After about six weeks of recording and training to code the videos with Solomon Coder (beta version 16.06.26) (Péter, 2016) the interobserver reliability was tested, as two observers worked together on the social network analysis. Both observers coded the same ten scan sampling videos and about 100 *ad libitum* recorded interactions. With these results the Cohen's Kappa was calculated and reached a value of 0.84 for the scan sampling videos and 0.90 for the *ad libitum* videos, indicating excellent agreement in both cases (Landis & Koch, 1977).

### 2.2.2 Data collection

For the social network analysis, two forms of samplings were conducted to record social interactions; scan samplings and *ad libitum* samplings. While scan sampling means that the behavior or location of all individuals of a group is scanned at regular intervals, *ad libitum* sampling means to record whatever seems to be relevant to answer the research question, as there is no constraint of what or when to record (Martin & Bateson, 2007).

Scan sampling took place from March 2016 to June 2016, at least three days a week, always between 8 am and 6 pm. Per day, four to six scan samples with a minimal interval of 30 minutes between two scans were conducted. During each scan sampling the whole group of pigs was recorded; mainly grouping behavior, but also sociopositive, socionegative or mating-related behavior was coded (Table 2). *Ad libitum* sampling of sociopositive, socionegative and mating-related behaviors of Table 2 took place between scan samplings. Videos were recorded with a camcorder (JVC GZ-RX601BE) and coded with Solomon Coder (Péter, 2016). In total 312 scans and 2063 *ad libitum* videos were recorded and coded.

### 2.2.3. Data analysis

The network analysis was conducted with CoSbiLab Graph software (Valentini & Jordan, 2010). The created networks are based on the measure of *centrality*, which considers the weights on the edges and the direction of interactions. Furthermore, the non-local neighborhood is also taken into consideration (Müller et al., 1999; Jordán et al., 2003).

Networks were visualized in Netdraw (Borgatti, 2002), and drawn by using the layout “spring embedding”, which means that densely connected nodes are tendentially clustered in the center of the networks and less connected nodes in the periphery around the center. However,

the layout algorithm not only puts the most connected individuals (nodes with higher centrality) in the center, it also tries to minimize crossings between the arrows. Hence, the most central individuals might be close to, but not exactly in the middle of the network (Croft et al., 2008).

Generally, networks were created for each behavior that is listed in Table 2. However, as the behaviors “gnashing of teeth” and “scent marking” do not require a direct receiver of the signal they cannot be visualized as network. Furthermore, these two behaviors are strictly male behaviors and will therefore be only compared between the male individuals of the group (litters born in 2014:  $N=8$ , and litters born in 2015:  $N=11$ ;  $N_B=5$ ,  $N_R=5$ ,  $N_Z=9$ ).

In addition to the networks of the separate behaviors, networks of the sums of sociopositive and socionegative behaviors were created. Sums of those two behavior groups were calculated by addition of all sociopositive, and all socionegative interactions respectively. Finally, the centrality indices for these sums were calculated. In addition to sociopositive and socionegative behaviors we also analyzed mating related and grouping behaviors (Table 2) separately, because these behaviors are important components of a pig’s natural behavioral repertoire but could not clearly be classified as sociopositive or socionegative.

As differences in the frequency of social interactions between the three age classes (Mother-sows:  $N=3$ , litters born in 2014:  $N=18$ , and litters born in 2015:  $N=20$ ) or the three families ( $N_B=14$ ,  $N_R=12$ ,  $N_Z=15$ ) in the social network were expected, Kruskal-Wallis tests and Dunn-Bonferroni post-hoc tests were conducted. Additionally, to test for differences of social interactions between the three adult mother-sows ( $N=3$ ) and their adolescent litters ( $N=38$ ) Mann-Whitney-U tests were conducted, using SPSS (version 23.0; IBM Corp., Armonk, NY, U.S.A.).

In order to extract the dyads that either had an affiliative or an agonistic relationship type, the behaviors that were most appropriate to indicate affiliative and agonistic relationships were required. As it might be possible that the pigs use different sociopositive behaviors in different social contexts it was necessary to conduct a principal component analysis (PCA). PCA is a tool to simplify multidimensional data and to find patterns in a dataset (Leveret al., 2017). The PCA revealed that three of the sociopositive behaviors of Table 2 “touching”, “snuffling” and “co-foraging” and additionally “grouping during foraging” load on one component. The same was done for socionegative behaviors, where four of the socionegative behaviors of Table 2 “fighting”, “gnashing”, “threatening” and “chasing alone” loaded on one component. Afterwards the sum of the four sociopositive behaviors that indicate an affiliative relationship and the sum of the four socionegative behaviors that indicate an agonistic



relationship was calculated. The mean numbers of both the four sociopositive and the four socionegative interactions over all dyads were calculated and were then used to define both relationship types. An affiliative relationship was required to have more than twice as many sociopositive interactions and less socionegative interactions than the previously calculated mean numbers. Dyads with agonistic relationships were required to have twice as many socionegative interactions than the mean number and less than the mean number of sociopositive interactions.

Both networks, one for the four sociopositive and one for the four socionegative interactions were also drawn in Netdraw (Borgatti, 2002) by using the layout “spring embedding”, but without the measure of centrality. The direction of interaction and weights on the edges were taken into consideration, but not the non-local neighborhood.

**Table 2. Ethogram for the social network analysis.**

Behavior	Abbreviation	Definition
<b>Sociopositive</b>		
Greeting	Gr	Vocalization and touching the other's snout. Sometimes also prodding, but only at each other's head
Snuffling	Su	Sniffing parts of each other's head
Touching	To	Direct contact of two pigs between the pig's snouts and other body regions
Co-feeding	Cf	Feeding next to each other at the feeding ground with not more than a radius of the individual's head apart
Co-foraging	Co	Looking for food next to each other or even eating next to each other at the fodder meadow with not more than a body length apart
Co-resting	Cr	Pigs lie next to each other, with body contact
<b>Socionegative</b>		
Displacement without body contact	Di	Rapid movement of the head of pig A towards pig B and pig B runs off. Pig B also runs off, when pig A comes near; sometimes accompanied by vocalization
Aggressive displacement without body contact	Ad	(Fast) direct approach of pig A towards pig B and pig B runs off
Displacement with body contact	Dw	Pig A displaces pig B with prodding, pushing or biting and pig B runs off
Threatening	Th	Two pigs walk shoulder to shoulder
Gnashing of teeth	Gn	Grinding with the teeth and foaming; sometimes also accompanied by vocalization
Fighting	Fi	Pig A and pig B push with their shoulders against each other, bite or scratch each other, sometimes there is also vocalization involved
Chasing alone	Ca	Pig A runs after pig B
Chasing in group	Cg	More than one pig runs after one individual; either with or without vocalization and/or biting
<b>Mating-related</b>		
Sniffing	Sn	A pig sniffs at another's bottom
Following	Fw	A male pig is running or going after a female pig
Scenting	Sc	A pig sniffs at the other's snout while the male is foaming; without vocalization
Scent marking	Sm	A male is setting a mark by rubbing the forelegs on the ground
Scenting while another male is copulating	Sw	A male is foaming and sniffs at the female's head while another male is copulating with that female
Prodding	Pr	A male prods or pushes the female's head and/or abdomen
Testing	Te	A pig is trying to mount a conspecific
Mounting	Mo	Pig A climbs on pig B's back, Pig B stands still but without copulation
Copulating	Cp	A male mounts a female and inserts his penis into the sow's vagina
<b>Grouping</b>		
Grouping during foraging	df	Pigs are in the same distance to each other and/or moving in the same direction while standing as well as feeding at the meadow or in the woods
Grouping during resting	dr	Pigs lying next to each other with not more than approximately one body length or width apart
Nearest neighbor	NN	Individual B is closest to individual A

### 2.3. Tolerated co-feeding tests

#### 2.3.1. Test subjects

By using the data of the social network analysis, the relationships between the pigs were investigated. Those relationships were then either defined as affiliative (see above) or agonistic and dyads with these relationship types were then selected based on their sex-combination. The test dyads were grouped in three categories: four male focal pigs with male test partners (same-sex dyads male), four female focal pigs with female test partners (same-sex dyads females), two male focals with female test partners and two female focals with male test partners (mixed-sex dyads) (Table 3). Altogether, 24 pigs, 12 males and 12 females, were tested. Some pigs participated as test partner for more than one focal pig and some focal pigs participated both as focal pigs and in another dyad as test partner.

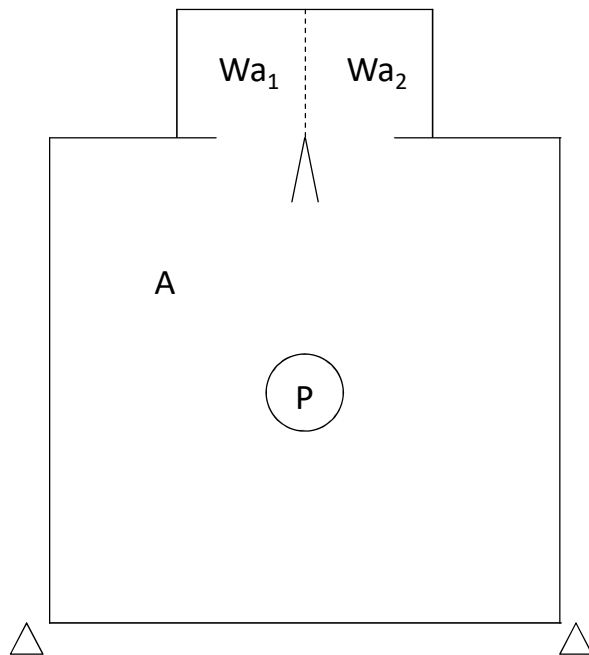
**Table 3. List of all tested dyads for the tolerated co-feeding tests.** The first partner in each cell shows the affiliative partner and the partner below is the agonistic partner (shown in bold type face). Numbers of interactions show the number of sociopositive (in dyads with an affiliative relationship) or socionegative (in dyads with an agonistic relationship) interactions.

Mixed-sex			Same-sex – males			Same-sex – females		
Focal (Sex)	Partner (Sex)	Number of interactions	Focal	Partner	Number of interactions	Focal	Partner	Number of interactions
B0 (♀)	Z1(♂)	12	B7	B12	16	B6	B0	14
<b>B0</b>	<b>Z4 (♂)</b>	<b>3</b>	<b>B7</b>	<b>R9</b>	<b>16</b>	<b>B6</b>	<b>R0</b>	<b>60</b>
B3 (♀)	Z9 (♂)	9	Z11	Z1	11	Z6	Z2	9
<b>B3</b>	<b>B12 (♂)</b>	<b>42</b>	<b>Z11</b>	<b>Z10</b>	<b>6</b>	<b>Z6</b>	<b>R0</b>	<b>8</b>
B13 (♂)	B1 (♀)	18	B2	Z1	14	B9	Z2	9
<b>B13</b>	<b>R1 (♀)</b>	<b>4</b>	<b>B2</b>	<b>R2</b>	<b>21</b>	<b>B9</b>	<b>Z12</b>	<b>3</b>
Z10 (♂)	Z2 (♀)	12	Z8	Z11	10	R11	R8	16
<b>Z10</b>	<b>B6 (♀)</b>	<b>3</b>	<b>Z8</b>	<b>R9</b>	<b>37</b>	<b>R11</b>	<b>B9</b>	<b>3</b>

#### 2.3.2. Test environment

The testing area consisted of two waiting areas (each 1.83 x 1.83 m), which were next to each other, but separated by a physical barrier that allowed only visual contact between the pigs, and the test arena (7.32 x 7.32 m) (Figure 1). The outside of the test arena was covered with visual covers. With small pieces of food, the focal pigs and its test partner were led to the waiting areas. To keep the motivation high for participating in the tests, highly attractive food-rewards were used like apple, bread or corn. If an individual was not motivated to participate in the tests or wanted to go back to the group or resting area this was granted immediately. The tests were repeated as soon as the individual seemed to be motivated again.

If an animal was not motivated for three days in a row, it was excluded from the experiment and replaced by another individual. This was not the case during the study.



**Figure 1. Testing area for the tolerated co-feeding tests:**  $Wa_1$  and  $Wa_2$  – waiting area 1 and 2 (for the focal pig and its test partner respectively), dotted line – physical barrier that allowed visual contact, A – arena, P – plate with the food. The triangles represent the position of the two video cameras.

### 2.3.3. General procedure

On the day before the first test session, each pig got a motivation session which consisted of five trials. In each motivation trial, the pig could feed on some corn, small pieces of apple and bread from a plastic plate (50 cm diameter), without the presence of a partner. After the pig had finished eating or if the pig was not interested in the plate anymore (30 seconds of no interaction), the experimenter called the pig back to the waiting area, then baited the plate again so the next trial could start. The pig was again released in the testing area four more times.

On the day after the motivation session was completed, the first of two test sessions was conducted. Test sessions consisted of six test trials each. On each test day, the focal pig was tested with both partners (affiliative and agonistic). The order of the affiliative or the agonistic test partner alternated per test day. On the first test day, the focal pig was first paired with the affiliative partner and then the agonistic partner, the next day vice versa and so on. Each pig started from the other waiting area than on the previous test day, to avoid possible influence of the testing order or the testing site. Before each test session, each pig got a motivation trial. In total, per partner two test sessions, which consisted of six trials each, were executed for all

dyads. To test for behavioral differences during the co-feeding tests caused by sow's heat, all mixed-sex dyads were tested again with the same procedure when the females were in heat. At the start of the test session, both pigs were first led in their respective waiting area. The plate, which was big enough that both animals could feed simultaneously, but small enough that it could be monopolized by one pig, was placed in the same distance (3.75 m) from each waiting area and the doors to the testing area were opened simultaneously by the experimenter (Figure 1). After the pigs had finished eating they were called back to their respective waiting area. Another trial started after baiting and placing the plate. After the sixth trial the focal pig stayed in its waiting area, while the first test partner was released back to the pasture and the other test partner entered the waiting area. Then again six trials were carried out, after which both pigs were released.

#### *2.3.4. Data collection and analysis*

Both, the motivation sessions and the test sessions were recorded by two camcorders (JVC GZ-RX601BE), each fixed to a tripod and positioned outside of the test arena (Figure 1). Videos were then coded for the behaviors, described in the ethogram for the tolerated co-feeding tests (Table 4). This was done with Solomon Coder software (Péter, 2016). As the trials had no standardized duration – because a trial always ended when the plate was empty, or the pigs were not interested in the plate anymore – the percentage of the feeding-related and proximity-related behaviors was calculated in relation to the total duration of the trials. The success rate of the feeding strategy “first at the plate” was calculated from the sum of the trials where the pig was first at the plate and was done for the focal pigs only.

Data was analyzed in SPSS (version 23.0; IBM Corp., Armonk, NY, U.S.A.). To test for differences between pigs with an affiliative relationship and pigs with an agonistic relationship on group level but also between groups (same-sex versus mixed-sex groups, mixed-sex in heat versus mixed-sex not in heat) Mann-Whitney-U tests were conducted.

As the Mann-Whitney-U tests for the influence of heat (please see 3.2.2 and subitems) and also the tests for the influence of the relationship (please see 3.2.1) and the influence of the sex (please see 3.2.3) were conducted on the same data set respectively, Bonferroni corrections were done ( $\alpha_a < 0.025$ ).

To test for our alternative prediction that dominance hierarchy could strongly influence the social interactions in co-feeding tests, we tested whether dominance influences the feeding strategy “first at the plate”, sociopositive and socionegative behaviors. Pigs were classified as dominant if they were able to successfully displace their test partners with body contact. If a

pig got displaced more often than it displaced the test partner it was classified as subdominant. For the feeding strategy the dominance of the focal individual over their both test partners was determined ( $N_D=10$ ,  $N_S=14$ ). For sociopositive and socionegative interactions the dominance of both pigs of each dyad was determined ( $N_D=24$ ,  $N_S=24$ ). Afterwards, Mann-Whitney-U tests were conducted to test for the influence of dominance.

**Table 4. Ethogram of the tolerated co-feeding tests.**

Behavior	Abbreviations	Definition
<b>Sociopositive</b>		
Touching	To	Direct contact of two pigs between the pigs snouts and other body regions
<b>Socionegative</b>		
Displacement without body contact	Di	Rapid movement of the head of pig A towards pig B, pig B runs off; also pig B runs off, when pig A comes near; sometimes with vocalization
Aggressive displacement without body contact	Ad	(Fast) direct approach of pig A towards pig B; pig B runs off
Displacement with body contact	Dw	Pig A displaces pig B with prodding, pushing and/or biting; pig B runs off
Attempts of displacement with body contact	Ag	Like displacement without body contact, but pig B shows no/less reaction to attempts of pig A; hence no displacement occurs
Severe aggression	Sa	Sum of displacement with body contact and attempts of displacement with body contact (Dw + Ag)
<b>Feeding-related</b>		
Co-feeding	Cf	Pigs feeding next to each other at the feeding plate
Feeding next to the plate	Fd	One pig is feeding from the plate, while the other one is really close (less than 15cm away with the snout from the plate) or even touches the plate (with the snout) and feeds next to the plate; “scrounging”
Feeding alone	Fa	Only one pig is feeding at the plate; the other pig is somewhere around in the arena
<b>Proximity-related</b>		
To be located within a body length	Bl	Pig A is at the feeding plate, pig B is within a distance of a body length to pig A
To be located within double body length	Db	Pig A is at the feeding plate, pig B is within a distance of the double body length to pig A
To be located in more than double body length	Mo	Pig A is at the feeding plate, pig B is more far away than the double body length
<b>Feeding strategy</b>		
First at the plate	Fp	The first pig at the feeding plate after synchronously opening the doors

## 2.4. Ethical consideration

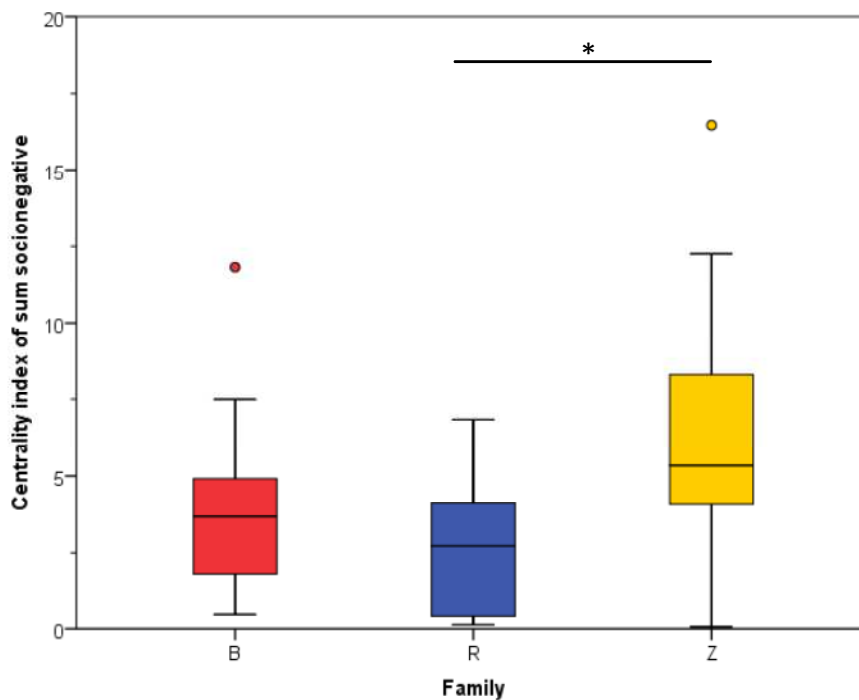
The institutional ethics and animal welfare committee at the University of Veterinary Medicine Vienna approved this study (ETK-02/09/2016) in accordance with national legislation (Animal Protection Act, BGBl. I Nr.118/2004, as amended from time to time) and Good Scientific Practice. Furthermore, as the present study was non-invasive (involving behavioral observations only) and stress free, and the subjects' participation was voluntary (encouraged by highly attractive food reward as positive reinforcement), it was not classified as an animal experiment requiring further permission under the Austrian Animal Experiments Act (Federal Law Gazette No. 501/1989).

### 3. Results

#### 3.1. Social network analysis

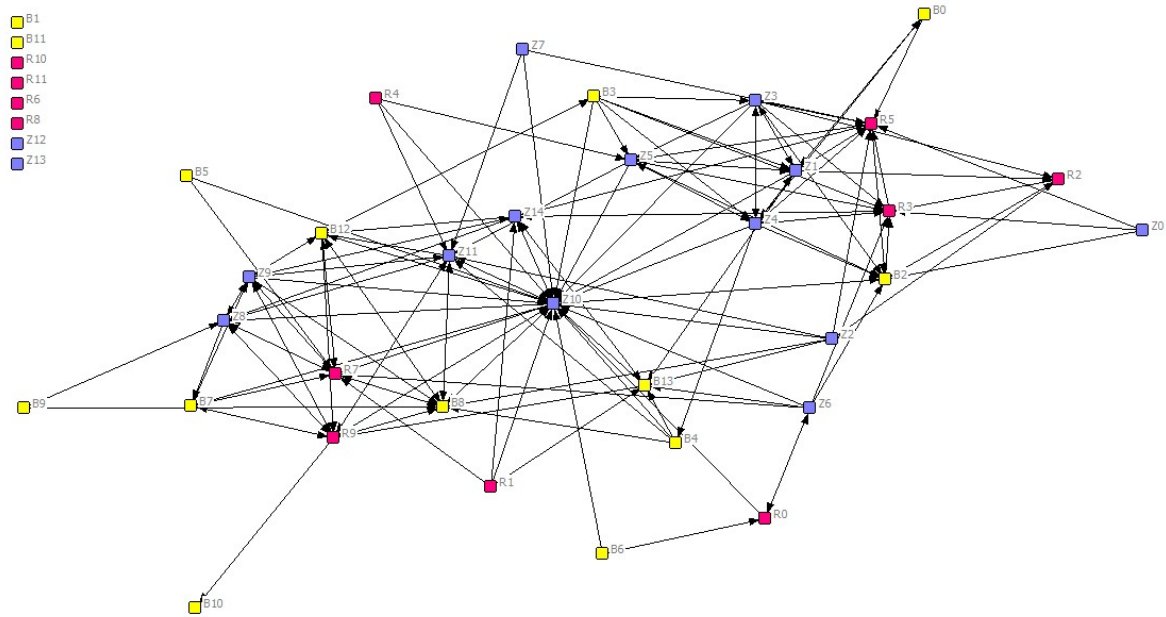
##### 3.1.1. Comparison of the three families

When taking into account the sum of all socionegative behaviors, the comparison between the three families revealed that pigs of the Z-family had significantly higher centrality scores than pigs of the R-family (Kruskal-Wallis test:  $N_B = 14$ ,  $N_R = 12$ ,  $N_Z = 15$ ,  $df = 2$ ,  $\chi^2 = 6.544$ ,  $p = 0.038$ ; Dunn-Bonferroni test: R-Z:  $\chi^2 = -2.529$ ,  $p = 0.011$ ) (Figure 2, Figure 3). In respect to all other behaviors there was no significant difference between the three families (Table A 8). But when taking into account the sum of all socionegative behaviors there was a slight tendency that pigs of the Z-family had significantly higher centrality scores than pigs of the B-family (Kruskal-Wallis test:  $N_B = 14$ ,  $N_R = 12$ ,  $N_Z = 15$ ,  $df = 2$ ,  $\chi^2 = 6.544$ ,  $p = 0.038$ ; Dunn-Bonferroni test: R-Z:  $\chi^2 = -1.530$ ,  $p = 0.130$ )



**Figure 2.** Centrality index of the behavior “sum of socionegative behaviors” of the three families B, R and Z.

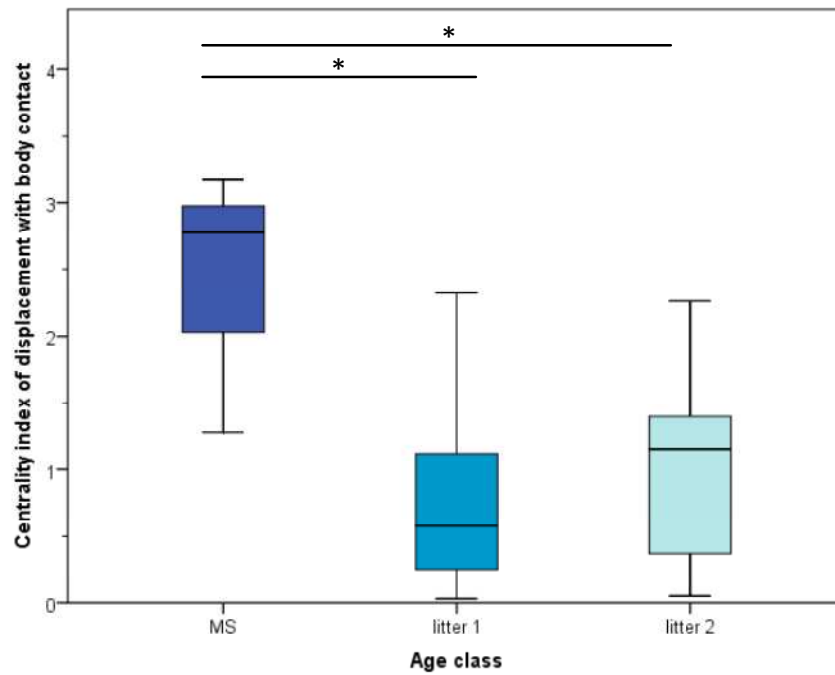




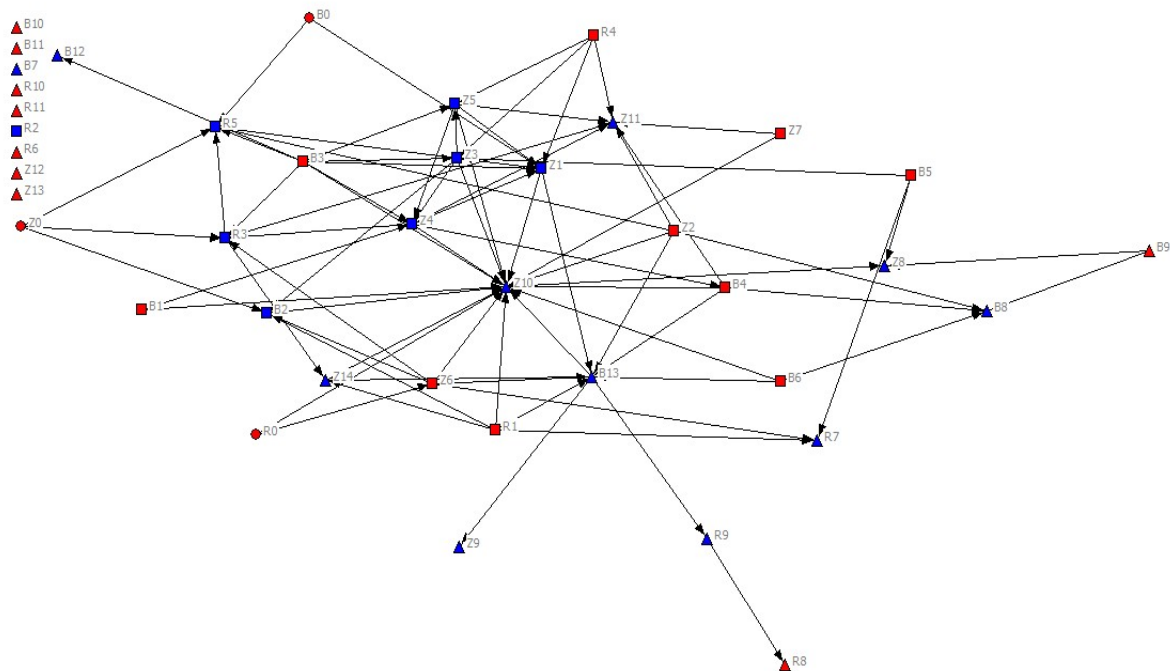
**Figure 3. Directed social network of “sum of socionegative behaviors”.** The arrows between the nodes represent more than five socionegative interactions. Nodes listed in the top left corner did not reach this criterion. Pigs of the B-family are shown in yellow, pigs of the R-family in pink and pigs of the Z-family are shown in blue.

### 3.1.2. Comparison of the three age classes

The comparison between the mother-sows (MS) and their litters born in 2014 (litter 1) and 2015 (litter 2) showed that mother-sows had significantly higher centrality indices when taking into account “displacement with body contact” than litters of both years (Kruskal-Wallis test:  $N_{MS}=3$ ,  $N_{litter1}= 18$ ,  $N_{litter2}= 20$ ;  $\chi^2 = 6.217$ ,  $p= 0.045$ ; Dunn-Bonferroni test: MS-litter1:  $\chi^2 = -2.477$ ,  $p= 0.010$ ; MS - litter2:  $\chi^2 = -1.994$ ,  $p= 0.046$ ) (Figure 4, Figure 5). In contrast, litters of both years had significantly higher centrality scores when taking into account “grouping behavior during foraging” compared to the mother-sows (Kruskal-Wallis test:  $N_{MS}= 3$ ,  $N_{litter1}= 18$ ,  $N_{litter2}= 20$ ,  $df= 2$ ,  $\chi^2 = 9.704$ ,  $p= 0.008$ ; Dunn-Bonferroni test: MS - litter1  $\chi^2 = 2.222$ ,  $p= 0.026$ ; MS - litter2  $\chi^2 = 3.020$ ,  $p= 0.003$ ) (Figure 6, Figure 7). For all the other behaviors there was no significant difference between the three age classes (Table A 9). But a slight tendency was found that litter 2 had significantly higher centrality scores than litter 1 when taking into account “grouping behavior during foraging” (Kruskal-Wallis test:  $N_{MS}= 3$ ,  $N_{litter1}= 18$ ,  $N_{litter2}= 20$ ,  $df= 2$ ,  $\chi^2 = 9.704$ ,  $p= 0.008$ ; Dunn-Bonferroni test: litter1 – litter2  $\chi^2 = -1.490$ ,  $p= 0.136$ )



**Figure 4.** Centrality index of the behavior “displacement with body contact” of mother-sows (MS), litters born in 2014 (litter 1) and in 2015 (litter 2).

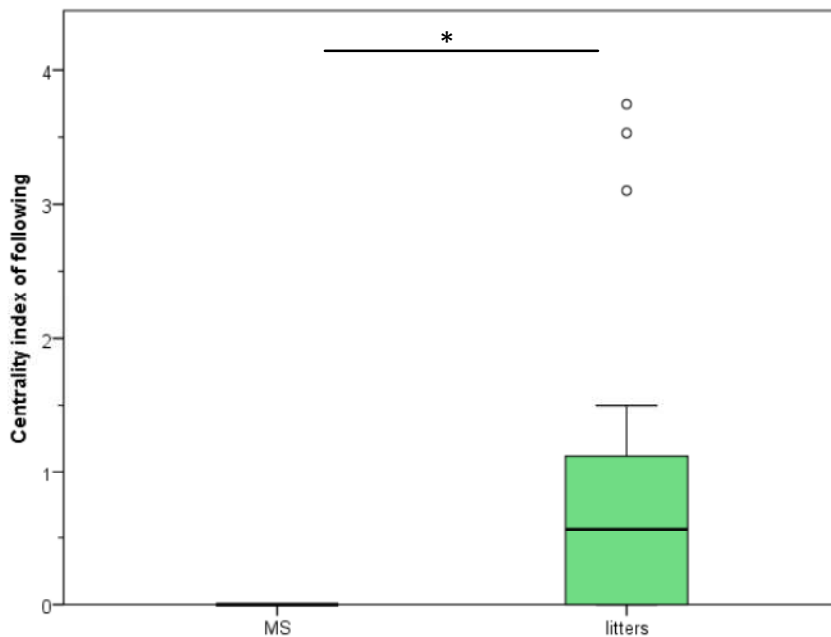


**Figure 5.** Directed social network of the socionegative behavior “displacement with body contact”. The arrows between the nodes represent more than three “displacements with body contact”. Nodes listed in the top left corner did not reach this criterion. Females are shown in red, males in blue. Mother-sows are represented as circles, individuals born in 2014 as squares and individuals born in 2015 as triangles.

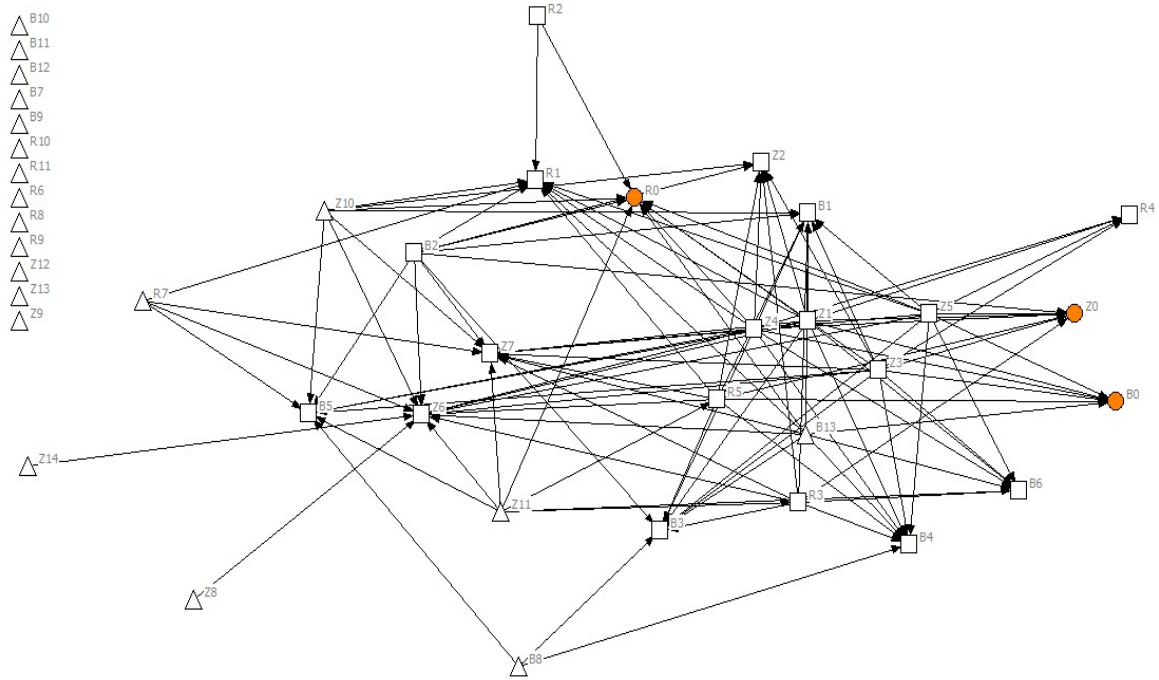


### 3.1.3. Comparison of the mother-sows against their litters

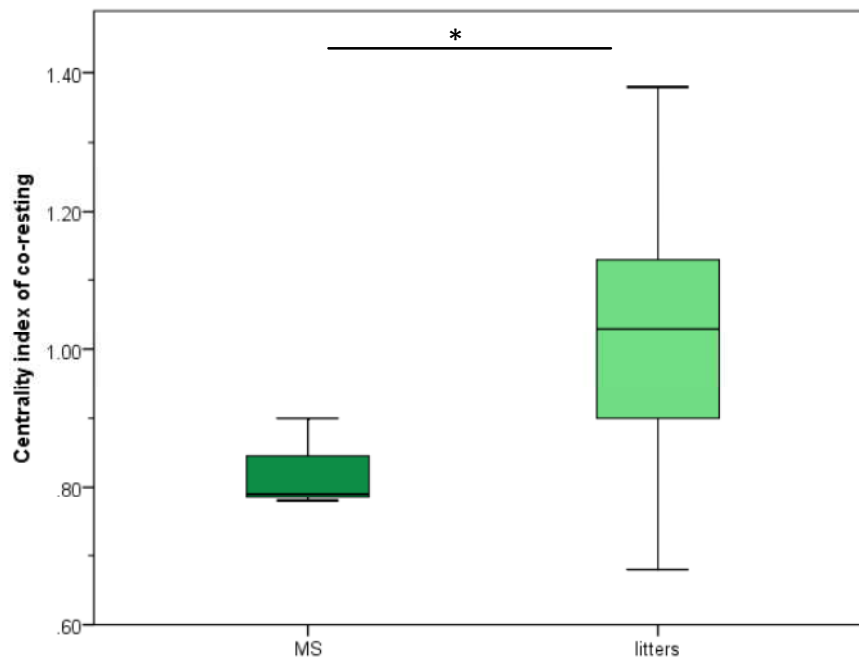
The comparison of mother-sows against their litters (born in 2014 and 2015) revealed that three mother-sows had significantly lower centrality indices when taking into account “following” (Mann-Whitney-U test:  $N_{MS}= 3$ ,  $N_{litters}= 38$ ;  $Z = 2.069$ ,  $p= 0.039$ ) (Figure 8, Figure 9), “co-resting” (Mann-Whitney-U test:  $N_{MS}= 3$ ,  $N_{litters}= 38$ ;  $Z = 2.179$ ,  $p= 0.029$ ) (Figure 10, Figure 11) and “grouping during foraging” (Mann-Whitney-U test:  $N_{MS}= 3$ ,  $N_{litters}= 38$ ;  $Z = 2.735$ ,  $p= 0.006$ ) (Figure 12, Figure 13) compared to their litters of both years. Opposed to this, mother-sows had significantly higher centrality indices when taking into account “displacement with body contact” (Mann-Whitney-U test:  $N_{MS}= 3$ ,  $N_{litters}= 38$ ;  $Z = -2.303$ ,  $p= 0.021$ ) compared to their litters of both years (Figure 14, Figure 15). There was no significant difference between the mother-sows and their litters of both years with regard to the other behaviors of the ethogram (Table A 10). But a slight tendency could be found for “displacement without body contact”, where mother-sows showed more displacements than their litters (Mann-Whitney-U test:  $N_{MS}= 3$ ,  $N_{litters}= 38$ ;  $Z = -1.628$ ,  $p= 0.103$ )



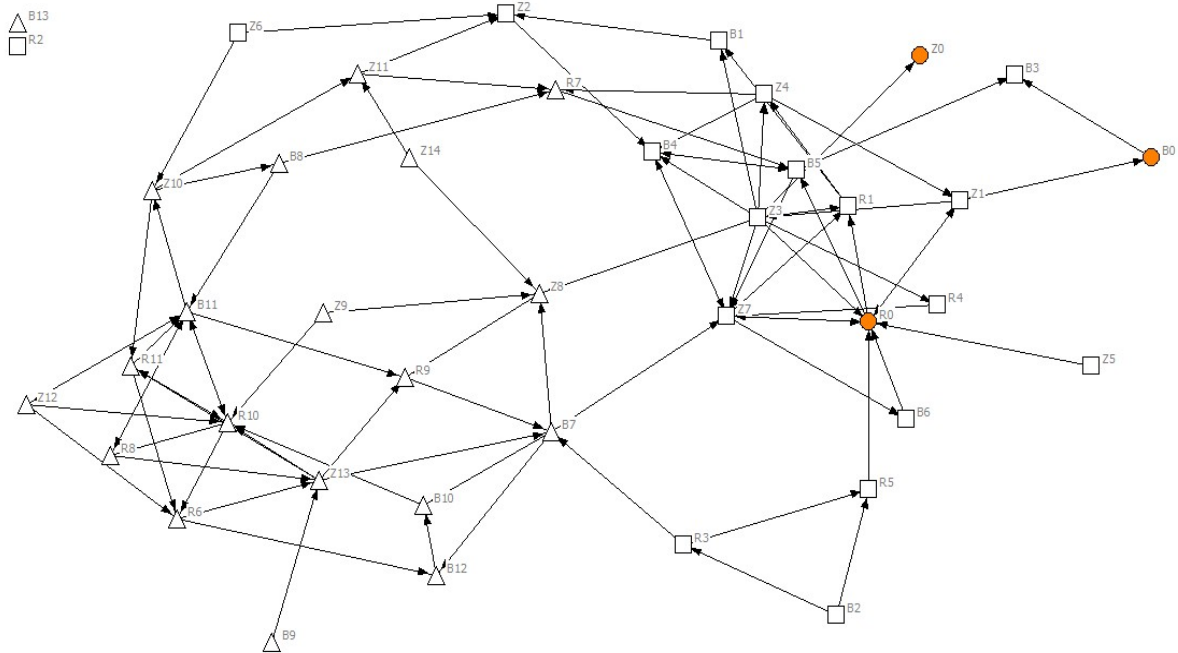
**Figure 8.** Centrality index of the behavior “following” of the mother-sows (MS) and their litters of both years.



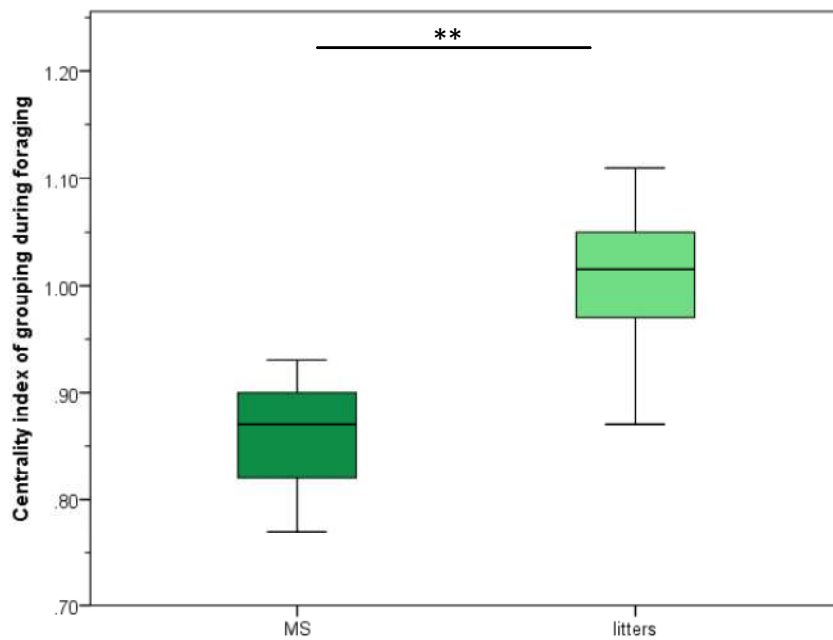
**Figure 9. Directed social network of the behavior “following”.** The arrows between the nodes represent more than three times “following”. Nodes listed in the top left corner did not reach this criterion. Mother-sows are represented as orange circles, individuals born in 2014 as squares and individuals born in 2015 as triangles.



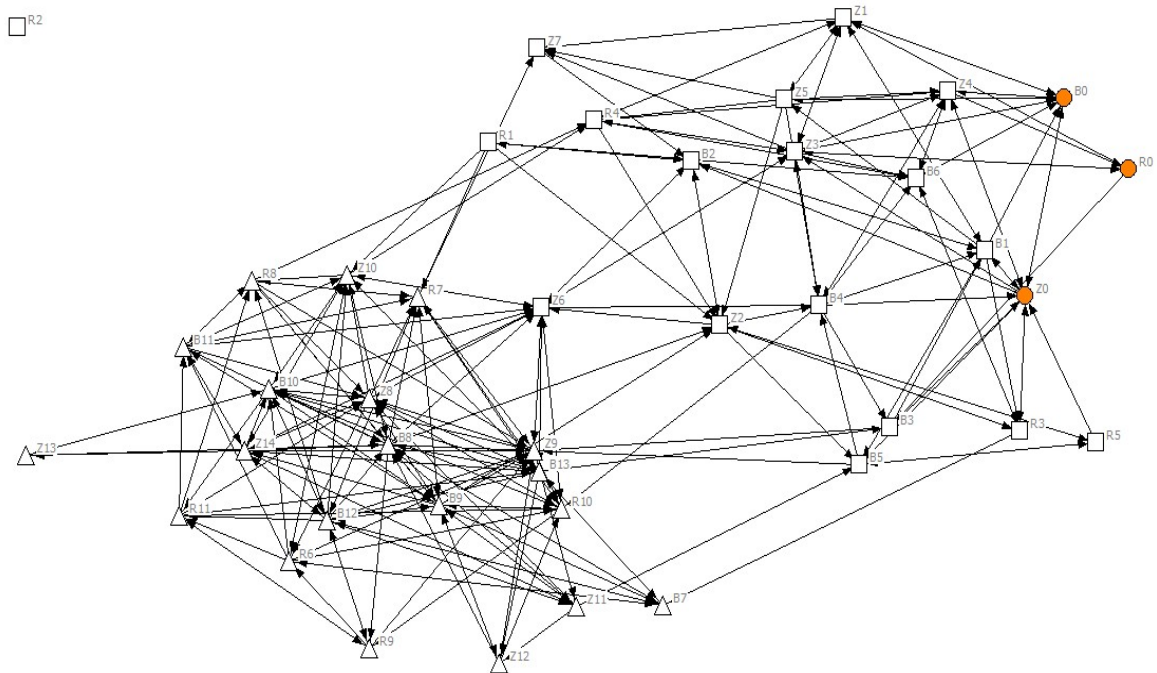
**Figure 10. Centrality index of the behavior “co-resting” of the mother-sows (MS) and their litters of both years.**



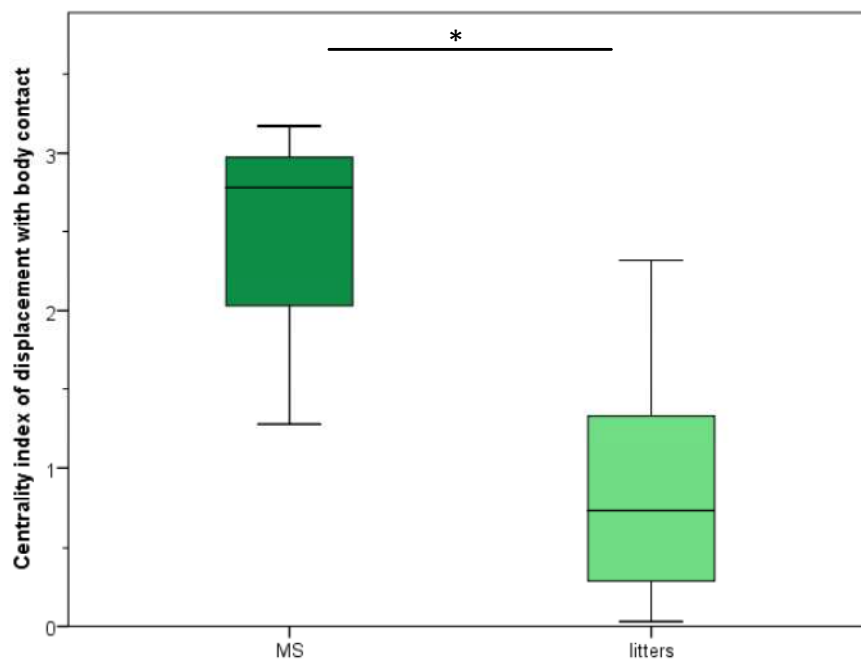
**Figure 11. Directed social network of the behavior “co-resting”.** The arrows between the nodes represent more than three times “co-resting”. Nodes listed in the top left corner did not reach this criterion. Mother-sows are represented as orange circles, individuals born in 2014 as squares and individuals born in 2015 as triangles.



**Figure 12. Centrality index of the behavior “grouping during foraging” of the mother-sows (MS) and their litters of both years.**



**Figure 13. Directed social network of the behavior “grouping during foraging”.** The arrows between the nodes represent more than five times the behavior “grouping during foraging”. Nodes listed in the top left corner did not reach this criterion. Mother-sows are represented as orange circles, individuals born in 2014 as squares and individuals born in 2015 as triangles.



**Figure 14. Centrality index of the behavior “displacement with body contact” of the mother-sows (MS) and their litters of both years.**







### 3.2. Tolerated co-feeding tests

In order to extract the dyads that either had an affiliative or an agonistic relationship type the mean numbers of both the four sociopositive and the four socionegative interactions over all dyads were calculated and were then used to define both relationship types.

An affiliative relationship was required to have more than twice as many sociopositive interactions and less socionegative interactions than the previously calculated mean numbers. Dyads with agonistic relationships were defined to have twice as many socionegative interactions than the mean number and less than the mean number of sociopositive interactions. The mean number of the four sociopositive interactions was 4.2, the mean number for socionegative interactions was 0.85. As a consequence, dyads that had nine (twice the mean number of sociopositive interactions) or more than nine sociopositive and less than two (twice the mean number of socionegative interactions) socionegative interactions were determined as having an affiliative relationship. Dyads that had more than two socionegative and less than nine sociopositive interactions were determined as having an agonistic relationship. Taking into consideration the three categories (same-sex females, same-sex males and mixed-sex dyads) to avoid possible influence of the sex, the 24 dyads listed in Table 3 have been chosen for the tolerated co-feeding tests.

The influence of the relationship type, of the sow's heat or of the sex of dyads with regard to the behavior in co-feeding tests was tested for all the 24 dyads.

#### 3.2.1. *Influence of the relationship of the test dyads ( $N_{Af}=12$ , $N_{Ag}=12$ )*

Dyads of both relationship types (affiliative versus agonistic) behaved similarly during the tolerated co-feeding tests, showing no significant differences in either sociopositive, or socionegative behaviors. Neither was there a difference with regard to the feeding strategy "first at the plate".

Dyads with an affiliative relationship did not spend significantly higher percentages of "co-feeding" compared to dyads with an agonistic relationship. Furthermore, neither the percentages of "feeding alone" nor "feeding next to the plate" was significantly different between dyads with affiliative relationships and dyads with agonistic relationships. The percentage of pigs staying "within a body length" to each other, "within double body length" or "more than double body length" away from each other did not differ significantly between dyads with affiliative relationships and dyads with agonistic relationships (Table A 11). However, there was a tendency that dyads with an affiliative relationship showed more sociopositive behaviors (Mann-Whitney-U test:  $Z = -1.905$ ,  $p = 0.057$ ;  $\alpha_a < 0.025$ )

### 3.2.2. *Influence of heat (N=8)*

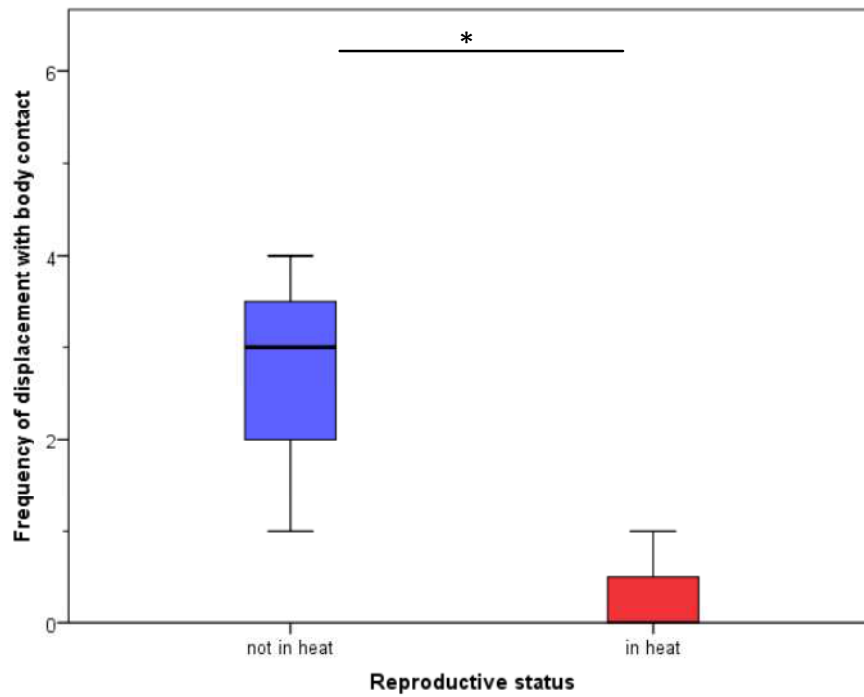
#### 3.2.2.1. Mixed-sex dyads with affiliative relationships (Af) versus dyads with agonistic relationships (Ag) when females were in heat ( $N_{Af}=4$ , $N_{Ag}=4$ )

Comparing dyads with an affiliative relationship and dyads with an agonistic relationship when females were in heat revealed no significant difference, neither in the feeding strategy nor in the frequency of sociopositive and socionegative behaviors.

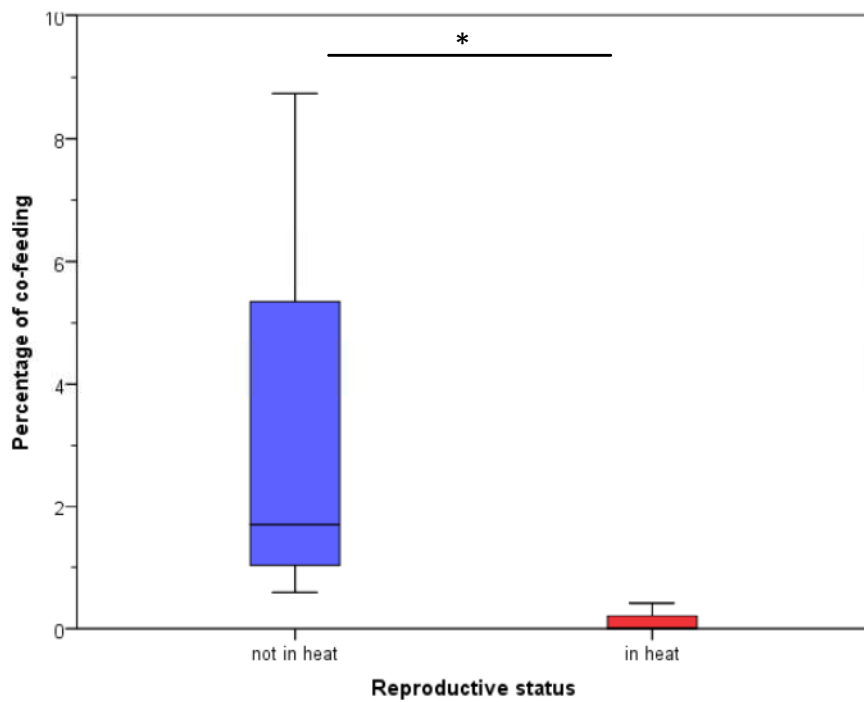
There was also no significant difference in the percentage of “co-feeding”, “feeding alone” or “feeding next to plate” between dyads with affiliative relationships and dyads with agonistic relationships when females were in heat. The percentage of “within a body length”, “within double body length” or “more than double body length” did also not differ significantly between dyads with affiliative relationships and dyads with agonistic relationships when females were in heat (Table A 12).

#### 3.2.2.2. Mixed-sex dyads with affiliative relationships when females were in heat (H) versus when females were not in heat (NH) ( $N_H=4$ , $N_{NH}=4$ )

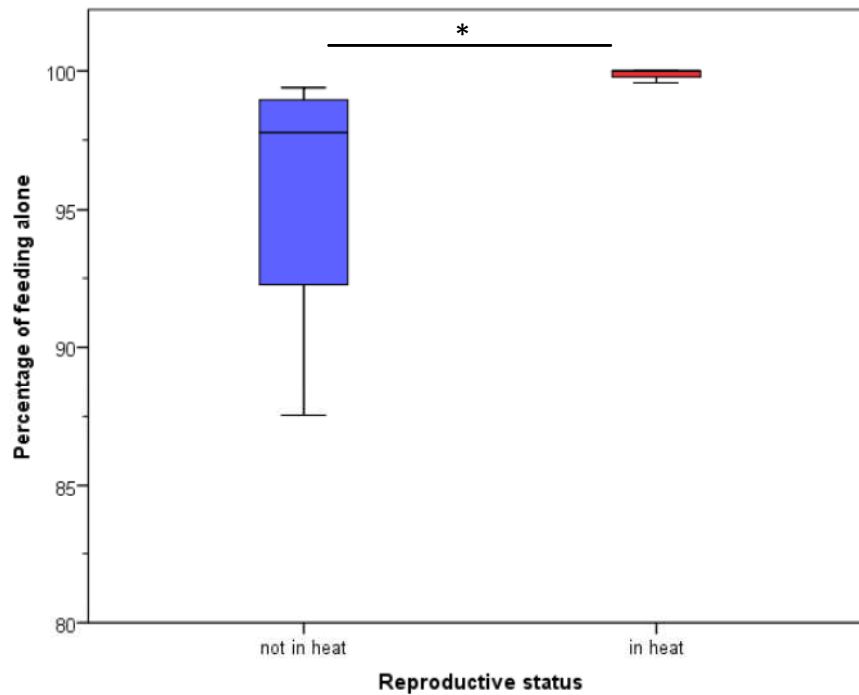
When females of mixed-sex dyads were not in heat there was significantly more “displacement with body contact” (Mann-Whitney-U test:  $Z = -2.247$ ,  $p = 0.025$ ;  $\alpha_a < 0.025$ ) (Figure 18) compared to when females were in heat. Dyads with an affiliative relationship did show significant lower percentages of “co-feeding” (Mann-Whitney-U test:  $Z = -2.366$ ,  $p = 0.018$ ;  $\alpha_a < 0.025$ ) (Figure 19), higher percentages of “feeding alone” (Mann-Whitney-U test:  $Z = -2.366$ ,  $p = 0.018$ ;  $\alpha_a < 0.025$ ) (Figure 20), but no significant difference in “feeding next to the plate” when the females were in heat compared to when they were not. There was also no significant difference in proximity-related behaviors when females were in heat than when not. Apart from “displacement with body contact”, all socionegative behaviors as well as sociopositive behavior and the feeding strategy were not influenced by the heat of females (Table A 13). But there was a tendency that dyads showed more severe aggression (Mann-Whitney-U test:  $Z = -1.947$ ,  $p = 0.052$ ;  $\alpha_a < 0.025$ ) when the females were not in heat.



**Figure 18.** Comparison of the frequency of “displacement with body contact” of dyads with affiliative relationships when females were not in heat versus when females were in heat.



**Figure 19.** Comparison of the percentage of “co-feeding” of dyads with affiliative relationships when females were not in heat versus when females were in heat.



**Figure 20.** Comparison of the percentage of “feeding alone” of dyads with affiliative relationships when females were not in heat versus when females were in heat.

### 3.2.2.3. Mixed-sex dyads with agonistic relationships when females were in heat versus when females were not in heat ( $N_H=4$ , $N_{NH}=4$ )

In mixed-sex dyads with an agonistic relationship the heat of the sows had neither an influence on the feeding strategy “first at the plate” nor on the sociopositive or socionegative interactions.

There was also no significant difference in the percentage of “co-feeding”, “feeding alone” or “feeding next to plate” between dyads with an agonistic relationship when females were in heat and when not. The percentage of “within a body length”, “within double body length” or “more than double body length” were also not influenced by the heat of the sows in dyads with an agonistic relationship (Table A 13). But there was a tendency that dyads showed more “displacement with body contact” (Mann-Whitney-U test:  $Z = -2.084$ ,  $p = 0.037$ ;  $\alpha_a < 0.025$ ) and more “severe aggression” (Mann-Whitney-U test:  $Z = -2.084$ ,  $p = 0.037$ ;  $\alpha_a < 0.025$ ) when the females were not in heat. Furthermore, there was a tendency that the dyads showed more “co-feeding” (Mann-Whitney-U test:  $Z = -2.033$ ,  $p = 0.042$ ;  $\alpha_a < 0.025$ ) and less “feeding alone” (Mann-Whitney-U test:  $Z = -2.021$ ,  $p = 0.043$ ;  $\alpha_a < 0.025$ ) when the females were not in heat.

### 3.2.3. *Influence of the sex of the test dyads (N=24)*

There was no significant difference between same-sex dyads ( $N_{ss}=16$ ) and mixed-sex dyads ( $N_{ms}=8$ ) with regard to sociopositive and socionegative behaviors. The feeding strategy was also not influenced by the sex of the tested dyads.

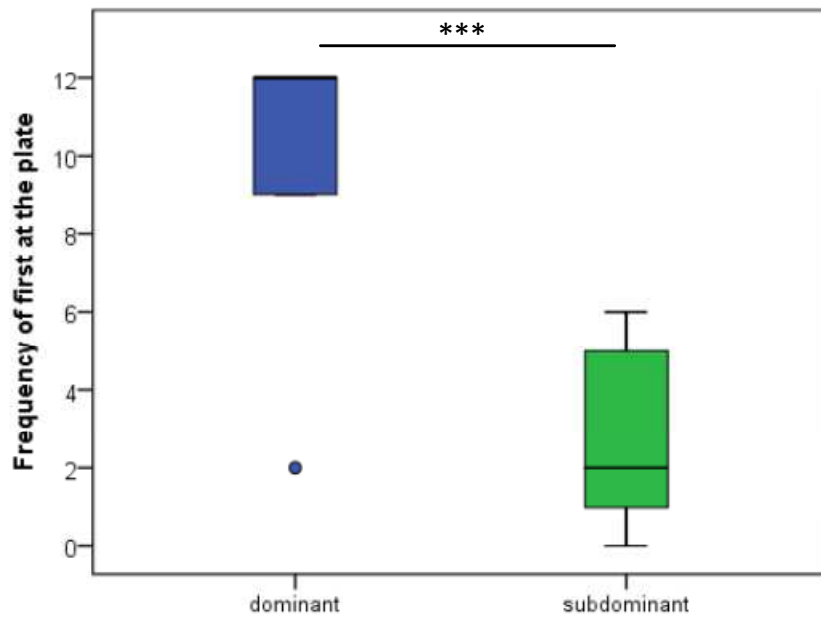
Same-sex dyads did not significantly differ from mixed-sex dyads neither with regard to feeding-related behaviors nor with regard to proximity-related behaviors (Table A 14).

### 3.2.4. *Influence of the dominance hierarchy*

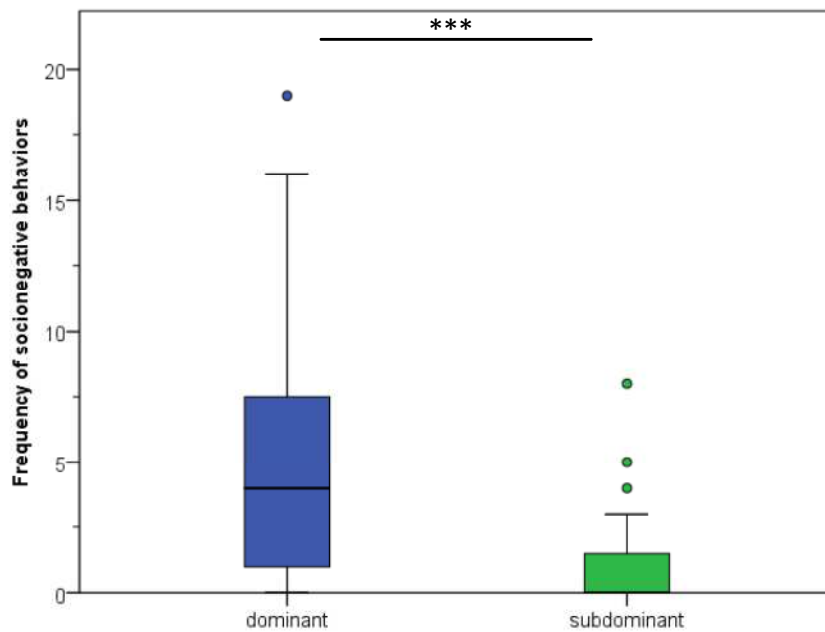
To examine the alternative hypothesis that the dominance hierarchy plays a more important role than the relationship type of dyads, it was tested whether there is a difference between dominant and subdominant individuals with regard to the feeding strategy “first at the plate”, as well as sociopositive and socionegative behaviors. Pigs were classified as dominant if they were able to successfully displace their test partners with body contact. If a pig got displaced more often than it displaced the test partner it was classified as subdominant.

The dominance hierarchy seems to have an influence, as dominant focal pigs were highly significant more often “first at the plate” compared to subdominant focal individuals (Mann-Whitney-U test:  $N_D=10$ ,  $N_S=14$ ;  $Z=-3.680$ ,  $p<0.001$ ) (Figure 21).

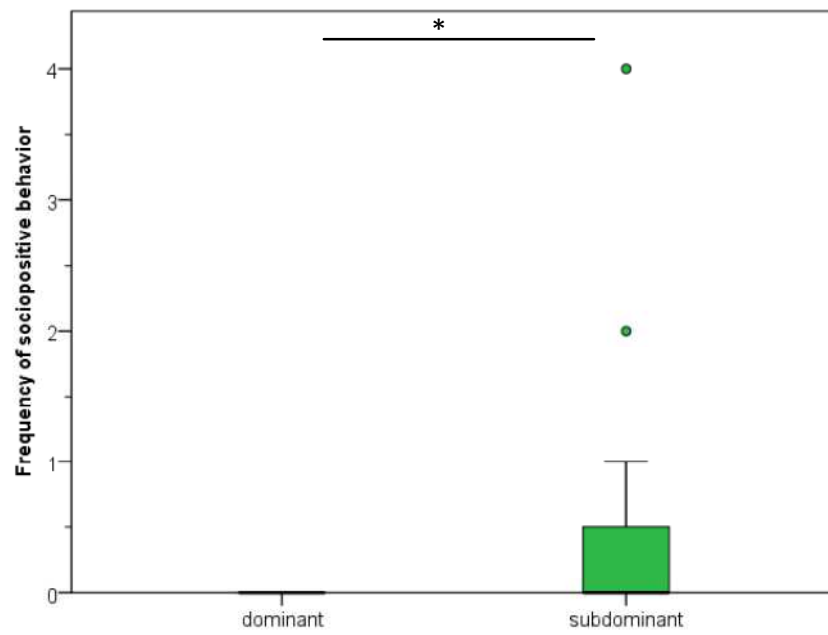
Furthermore, dominant individuals did show highly significant more socionegative behaviors compared to subdominant individuals (Mann-Whitney-U test:  $N_D=24$ ,  $N_S=24$ ;  $Z=-3.773$ ,  $p<0.001$ ) (Figure 22). In contrast, subdominant individuals showed significantly more sociopositive behavior compared to dominant individuals (Mann-Whitney-U test:  $N_D=24$ ,  $N_S=24$ ;  $Z=-2.586$ ,  $p=0.010$ ) (Figure 23).



**Figure 21.** Frequency of successful attempts of the feeding strategy “first at the plate” of dominant (N=10) and subdominant (N=14) focal pigs.



**Figure 22.** Frequency of socionegative behaviors during the tolerated co-feeding tests of dominant (N=24) and subdominant (N=24) individuals.



**Figure 23. Frequency of sociopositive behavior during the tolerated co-feeding trials of dominant (N=24) and subdominant (N=24) individuals.**



## 4. Discussion

### 4.1. Social network analysis

There was support for the hypothesis that social interaction patterns differ from randomness and that there are also individual differences. It has been found that the three families differ in the way how they interact with conspecifics. Individuals of the Z-family showed significantly more socionegative behaviors than pigs of the R-family (and tendentially more than pigs of the B-family). This could be an indicator that individuals of the Z-family might be dominant over individuals of the other families, as socionegative behaviors include mainly aggressive behaviors like displacements or fights for example.

Contrary to our expectation most differences in social interactions were not between all three age classes but only between the mother-sows and their litters. Comparisons of the mother-sows, the litters born in 2014 and the litters born in 2015 revealed, that mother-sows showed significantly more “displacement with body contact” and tendentially more “displacement without body contact” than the litters born in 2014 but also than the litters born in 2015. The reverse is true for “grouping during foraging” where the litters born in 2014 and also the litters born in 2015 showed significantly more frequently grouping behavior than the mother-sows did. Furthermore, litters from both years showed more “co-resting” than their mothers did. It seems that mother-sows are more solitary, as they showed less grouping behavior during foraging and also during resting. At the same time they showed more “displacement with body contact” and tendentially more “displacement without body contact” compared to their litters of both years, which could indicate that the litters are subdominant to their adult mother-sows. This finding is in line with the finding of Newberry & Wood-Gush (1986) that sows are dominant over their subadult offspring. Furthermore, the study of Newberry & Wood-Gush (1986) has shown that pigs of the same litter interact a lot with each other and also, but to a lower degree, with pigs of other litters, which would explain why mother-sows seem to be more solitary. Allwin et al. (2016) found in wild boars (*Sus scrofa*) that mature individuals were less active than immature ones. So it could be possible that the different activity patterns of the adult sows and their litters could also have impact on the differences we found with regard to grouping behavior. However, these results have to be treated with caution, because here a major point for discussion is the big difference in the sample sizes.

To test for differences between the adult mother-sows (N=3) and their subadult and juvenile offspring (N=38) we had to test with very different sample sizes. It might be possible that the differences between mother-sows and their litters could also be caused by the fact that the group of mother-sows consisted of females only while the group of offspring consisted of

females and males. Another factor that could have influenced the behavior of the mother-sows is the personalities or the fact that the three mother-sows are sisters and therefore may behave more similar than individuals of a bigger group with many different personalities and different behaviors of also non-related individuals, because this could cause the neutralization of individual differences in a bigger group.

It would have been better for the validity of the results to avoid such possible influences and therefore test with more balanced sample sizes but this was not possible here, due to restrictions caused by the composition of the group. However, the natural group composition of pigs in matriline sounders, where a few females live together with their offspring, is more valid to gain knowledge about their social lives under natural or semi-natural conditions than for example comparing a group of adult sows against a group of sub-adults and juveniles of the same sample size under artificial conditions.

Not only are there differences in behavioral patterns like activity or centrality, we could also find clear evidence for different types of relationships (affiliative, agonistic and neutral) within the social structure of our group. This is in line with former studies where different relationship types have been found, for example in female feral goats (Stanley & Dunbar, 2013), in cattle (Reinhardt & Reinhardt, 1983), in common ravens (Schwab et al., 2008; Loretto et al. 2012) and in red grouse (Watson et al., 1994). We were able to detect a distinct difference between those relationship types and to define subject animals with both, affiliative and agonistic partners for the following tests.

A possible point for discussion is the method of defining the different relationship types, because instead of using only certain sociopositive and socionegative behaviors to determine affiliative and agonistic relationship types, it is possible to use the sum of all sociopositive or of all socionegative interactions. However, the PCA revealed that the subjects of our sample used different sociopositive behaviors in different social contexts. Therefore, instead of using the sum of all sociopositive interactions, only three of the sociopositive interactions and additionally grouping behavior during foraging were appropriate to indicate affiliative relationships. The same is true for agonistic relationships that were best indicated by four socionegative interactions.

The calculation of the average of sociopositive and socionegative interactions revealed that sociopositive interactions were shown more frequently than socionegative interactions (mean sociopositive interactions was 4.2 and mean socionegative interactions was 0.85). This is in line with Stolba & Wood-Gush (1989) who also found that sociopositive behaviors were frequently shown while socionegative behaviors occurred rarely.

It is important to note that the relationship types varied considerably. The amount of socionegative interactions of the chosen test dyads with an agonistic relationship varied from three to 60. Interestingly, the highest number of socionegative interactions was not shown by males, as one may expect, it was shown by two females (R0 and B6). During the period of behavioral observations, these two females were frequently seen fighting or threatening each other. We assume that the adolescent B6 tried to challenge the adult R0 to get her position in the dominance hierarchy. Few months after data collection was completed the fights between the two females stopped. Between B3 and B12, a mixed-sex dyad, we observed 42 socionegative interactions that mainly consisted of threatening and fighting. Z8 and R9 also showed high frequencies of socionegative interactions. Because Z8 and R9 are same-aged males, we assume that the 37 socionegative interactions also resulted from fights for their positions in the dominance hierarchy.

There is also variation in the frequencies of sociopositive interactions of the chosen test dyads with an affiliative relationship, although the variation here is not as big as it is for the socionegative interactions (variation from nine to 18 sociopositive interactions). 18 sociopositive interactions were the highest frequency of all the test dyads and were observed between B13 and B1, a mixed-sex pair. B13 and B1 were frequently observed at co-foraging at the pasture. B7 and B12, same-aged males, and R11 and R8, same-aged females, showed 16 sociopositive interactions each. B7 and B12 were frequently observed at co-foraging at the pasture, while R11 and R8 were frequently observed at touching and foraging together in the same group. As both dyads are litter mates, the finding that they spend more time together during foraging (co-foraging or at least in the same group) is in line with Newberry & Wood-Gush (1986), who also found juvenile littermates tend to spend more time together. Still, all the chosen dyads fit in the criterion of at least nine sociopositive and less than two socionegative interactions for affiliative and at least two socionegative and less than nine sociopositive interactions for agonistic relationships.

Interestingly, the majority of dyads with an affiliative relationship are composed of siblings (more than 66%) and the majority of dyads with an agonistic relationship are composed of non-siblings (more than 83%). This is in line with Schwab et al. (2008) who found in common raves that siblings spent more time in close proximity than non-siblings. It also fits the findings of Loretto et al. (2012) that aggression in common raves is more frequent between non-kin.

#### **4.2. Tolerated co-feeding tests**

An interesting and important finding of this thesis is that the data from the field observations and the data from the co-feeding tests diverge, at least at the group level. Therefore there is no evidence that social network data taken through regular observations will provide the same insight into a social group than a behavioral experiment would do, as relationships found in natural conditions on the pasture did not persist also in artificial conditions in the co-feeding tests.

At group level the social relationship of pigs did not influence the behavior of the individuals in the artificial test situation; feeding- and proximity-related behaviors, the feeding strategy “first at the plate”, as well as sociopositive and socionegative behaviors did not significantly differ if the partner was an affiliate or not. A possible explanation for this could be the completely different (social) context. The data for the social network analysis was collected in semi-natural conditions on the pasture during mostly peaceful situations without any reason for competition, which is a completely different context than the artificial context in the testing arena where the pigs compete for a monopolizable food resource. The latter is a situation which our subjects only very seldomly experience in their daily life, as they feed mostly on the large pasture, or, during feeding time, on an area large enough that every animal can find enough of the provided food. So it is possible that the concept of “friendship” in pigs with affiliative relationships does hold on pasture only but not in situations where the pigs have much less space available. This would be consistent with DeVries et al. (2004) who found that cows while feeding prefer higher distances between each other, given that they had the possibility to do so. If they had less space available while feeding, the rate of aggressive behavior increased and the feeding rate decreased.

Another factor that could have influence on the social interactions in the co-feeding tests could be the highly attractive food that was used as reward. While the grass on the meadow is available all the time, the food reward used in the co-feeding tests is restricted, even during test situation, where only a small amount was provided. So eventually, independent of the type of the relationship the pigs have with their test partner, they might be more motivated to compete for food they highly prefer and that is available for a short time only compared to grass which is available all the time. To test for that kind of influences, one could repeat the test setting with either a low-value but still monopolizable food source, attractive food that is offered widespread, or without any offered food during test sessions at all, while measuring only proximity data and interactions in the relatively small compartment.

Instead of the relationship type, the dominance affected the behavior in tolerated co-feeding tests. Dale et al. (2017) found that in a group setting of co-feeding in gray wolves (*Canis lupus*) and domestic dogs (*Canis lupus familiaris*), feeding behavior was mainly influenced by the rank of the individuals and less by the type of the social relationship. According to Kaufmann (1983), dominance is defined as a relationship between two individuals where one individual is imperious over the other one in competitions. In pigs, it has been shown that dominance hierarchy regulates the access to food (Puppe, 1998) and that dominance-related aggression occurred more frequently in situations where food was available and additionally limited in time or space (Spinka, 2002). It seems plausible that also in our co-feeding tests, where the feeding behavior was not influenced by social relationship at group level, dominance hierarchy plays a more important role than the type of social relationship.

A tactic for subdominant individuals to gain more food or access to food at all could be trying to be first at the food source. In long-tailed macaques (*Macaca fascicularis*) dominance had no influence at the order of arrival of the food source but being first at the food source led to increased food consumption (Dubuc & Chapais, 2007). This is in contrast to our results, where dominance hierarchy seems to have an influence, as dominant pigs were significantly more often first at the food source. Our results are more in line with the study of Dale et al. (2017) where the dominant wolves arrived first at the food source more frequently than subdominant wolves. It seems like the subdominant tends to avoid the conflict with the dominant and prefers to lose all the food over going into a fight.

The explanation that the influence of dominance is more important than the type of the relationship between two pigs could also be used to explain why there was no influence of the relationship on sociopositive and socionegative behaviors. In this study, dominant individuals did show significantly more socionegative behaviors compared to subdominant individuals. Furthermore, subdominant individuals showed significantly more sociopositive behavior. An explanation for this could be that subdominant individuals showed appeasement behavior, which involves sociopositive behavior, to reduce aggressive behaviors (Keltner & Potegal, 1997) of their dominant test partners. Hence, it could be possible that subdominant individuals tried to propitiate their dominant test partners, to reduce the tendency for aggressive behavior or maybe also to increase their chances to co-feed.

Among others, Stevens & Gilby (2004), Kaplan & Hill (1985) and Brosnan & deWaal (2002) hypothesized that food sharing may occur for mating opportunities. In this study, we could not find support for this hypothesis as the test dyads did not show increased percentages of “co-feeding” or “feeding next to the plate” when the females were in heat compared to when

they were not. A possible explanation for this could be that the co-feeding tests with females in heat took place after the test sessions when females were not in heat. So it might be possible that the pigs have learnt in the first trials of the co-feeding tests when the females were not in heat, that they do not have much success in the competition with their dominant test partner in gaining accesses to the food source. Consequentially, the subdominant individuals did not try as hard as in the first trials to gain accesses to the food in the second sessions of tests when females were in heat as they did not get accesses to food in the first sessions. Unfortunately, we could not counterbalance the order of the tests due to time restrictions, because all females paused their heat cycle naturally during summer season. The role of mating behavior on social behavior like proximity and co-feeding might still be minor compared with pure hierarchy.

Meese & Ewbank (1973) described dominance hierarchy as strong, stable relationships. In order to reduce stressful encounters, pigs have to learn to behave adequately according to the dominance hierarchy (Arey & Franklin, 1995). It seems likely that once the pigs determined the dominance hierarchy, they act according to it and there is no need to fight in each encounter of the two test partners equally in which situation they are, daily life on the pasture, test situation, or during mating season. An indicator for this argument could be that dyads with an affiliative relationship as well as dyads with an agonistic relationship showed significantly lower percentages of “co-feeding” and higher percentages of “feeding alone” when females were in heat compared to when females were not in heat. That the pigs learnt about their chances to gain food from the monopolizable source if paired with a dominant partner in the first trials could also be the explanation for the finding that there was significantly more “displacement with body contact” in dyads with affiliative relationships in the first sessions compared to the second session 12 to 14 weeks later. The same has been found in dyads with agonistic relationships with the exception that also “severe aggression” was more frequently shown in the first session. So it seems plausible that the pigs tried to get access to the food in the new setting of the co-feeding tests in the new arena and once it was clear that the food source was monopolized by the dominant, they stuck to their strategy of avoiding conflict and subdominant individuals did not even try to get accesses to food anymore but stayed in the outer regions of the arena.

In general, the small sample size as a result of the classification of a focal pig with an affiliative and an agonistic partner and additionally the classification of the three sex-classes of test dyads (mixed-sex, same-sex male and same-sex female) limited the number of possible test dyads which might also have had an impact on the results. Hence, it would be interesting

to repeat those tests with dyads of both relationship types but instead of choosing them accordingly to their sexes choosing them accordingly to similar positions in the dominance hierarchy and, if possible, to increase the sample size.

Nevertheless, social network analysis provided a more subtle and deeper insight in the social structure of the group of pigs, as it gives us information of nearly all different contexts of the social life. Behavioral experiments on the other side can only cover very few aspects of the complex interactions in a dense social network. An experiment is mostly somehow restricted to certain contexts of the natural social life and can hardly encompass all the different contexts. Hence, social experiments based on behavioral observations must be designed carefully and possible effects of present (or not present) conspecifics or resources must be taken into account. Still, if the aim is to investigate complex social behaviors which are based on social relationships, it is absolutely necessary to conduct detailed behavior observations beforehand. Assessing social data only during experimental settings might lead to misinterpretations of results. The same might be true for a semi-natural setting compared to an artificial and restricted farm-housed condition; in the latter, possible social relationship types might be overridden by hierarchy or space restrictions. In our study, we identified Social Network Analysis as a very sensitive measurement for social structure and social relationships of our group of pigs and therefore as an essential tool for social behavior research.

But it is important to keep in mind that within the scope of this study only individuals of a single group of pigs were observed and tested. This causes limitations with regard to generalizations and conclusions of our results. It might be possible that a group of pigs of a different breed or even another group of Kune Kune pigs behave differently than the group in our study did. Hence, it would be very interesting, to repeat this study with other Kune Kune groups but also with groups of other breeds to see if there are behavioral differences compared to the group in our study.

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**A 1. Centrality indices of the behaviors of the ethogram of Table 2 for the individuals of the B-family (cf and cg were not shown).**

ID	gr	su	to	co	cr	di	ad	dw	th	gn	fi	ca	sn	fw	sc	sm	sw	pr	te	mo	cp	df	dr	sum_pos	sum_neg
<b>B0</b>	1.92	0.44	0.59	1.20	0.78	2.31	0.33	3.17	0.17	0.00	0.00	1.33	0.55	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.93	0.91	3.58	4.66
<b>B1</b>	0.44	0.57	0.25	0.93	0.91	0.31	0.00	1.27	0.00	0.00	0.50	0.00	0.64	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.05	0.88	2.58	1.79
<b>B2</b>	2.71	0.25	0.68	1.01	1.01	0.00	0.00	0.86	0.00	0.00	0.71	0.00	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.13	3.65	0.82
<b>B3</b>	2.00	0.25	0.10	0.82	1.06	0.00	0.00	0.22	0.09	0.00	0.15	1.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.97	1.05	3.21	0.46
<b>B4</b>	1.82	0.60	1.30	1.10	1.08	0.14	0.00	0.25	1.55	1.00	1.86	0.20	1.49	0.55	0.11	0.00	0.10	0.26	0.08	0.00	0.00	0.97	1.15	3.80	4.36
<b>B5</b>	0.76	4.08	1.35	1.27	0.95	0.27	0.00	1.12	1.54	0.00	1.72	1.67	2.61	1.14	0.76	0.00	0.60	1.16	3.67	1.60	0.33	1.06	1.04	5.58	3.70
<b>B6</b>	0.47	1.81	1.81	1.14	0.93	2.21	1.33	1.99	0.75	1.33	1.94	0.70	1.60	1.13	0.85	0.00	0.10	2.80	1.00	0.43	0.49	1.04	0.92	5.21	6.45
<b>B7</b>	0.50	0.18	0.10	0.93	0.84	0.84	0.50	1.15	0.13	0.00	0.66	0.33	0.44	0.12	0.00	0.00	0.00	0.29	0.00	0.00	0.00	1.05	0.86	2.34	7.49
<b>B8</b>	0.16	0.07	0.60	1.01	1.25	0.93	1.25	1.50	0.00	0.00	0.33	2.36	0.53	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.05	1.14	3.23	3.65
<b>B9</b>	1.20	0.69	0.52	0.84	1.14	0.79	1.28	1.70	0.00	0.00	0.28	0.20	0.70	0.20	0.00	0.00	0.00	0.17	0.00	0.00	0.00	1.11	0.98	3.15	2.74
<b>B10</b>	0.17	0.48	0.20	0.77	0.83	0.49	0.14	1.97	0.33	0.00	1.38	2.44	0.59	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	1.05	0.79	2.32	11.83
<b>B11</b>	0.89	1.89	2.05	0.96	1.10	0.00	0.00	0.12	1.74	0.00	0.59	0.33	1.06	1.12	0.00	0.00	0.00	1.21	0.00	0.00	0.00	0.94	1.09	3.89	2.43
<b>B12</b>	0.90	1.71	1.69	1.29	1.13	0.00	1.00	0.47	1.37	1.00	0.94	1.33	1.71	3.53	0.40	0.00	0.10	0.67	5.46	0.52	0.31	0.94	1.02	6.15	4.91
<b>B13</b>	1.88	0.07	0.33	0.88	1.05	0.37	0.00	0.57	0.60	0.00	0.50	1.14	0.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.08	1.02	2.78	1.67

**A 2. Centrality indices of the behaviors of the ethogram of Table 2 for the individuals of the R-family (cf and cg were not shown).**

ID	gr	su	to	co	cr	di	ad	dw	th	gn	fi	ca	sn	fw	sc	sm	sw	pr	te	mo	cp	df	dr	sum_pos	sum_neg
R0	0.14	0.50	0.22	0.70	0.79	0.75	0.33	1.28	2.33	0.00	2.50	0.50	0.42	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.77	1.09	2.14	6.84
R1	0.31	0.78	0.58	0.70	0.93	0.00	0.92	1.67	0.27	0.00	0.83	1.11	0.96	1.50	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.97	0.85	2.66	3.83
R2	1.64	0.27	0.21	1.19	0.98	0.00	0.50	0.03	0.00	0.00	0.11	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.07	0.89	3.76	0.14
R3	1.82	1.21	1.22	0.88	1.10	0.00	0.00	0.30	0.33	0.00	0.62	0.00	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.01	0.96	3.56	0.62
R4	0.00	0.18	1.71	0.56	1.17	0.11	0.42	0.43	0.45	0.50	0.93	0.00	1.91	1.25	3.05	0.00	0.10	4.35	1.56	0.00	0.00	1.02	1.23	2.09	1.55
R5	0.58	1.42	0.93	1.14	0.92	1.57	0.53	0.60	1.36	0.83	1.06	0.14	1.84	1.03	0.68	0.00	0.27	1.09	0.70	0.96	0.94	0.99	0.85	4.80	2.79
R6	0.52	0.90	0.31	0.71	0.87	2.98	2.17	1.35	0.00	0.00	0.00	0.36	0.47	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.07	1.01	2.62	3.56
R7	0.70	0.91	1.22	1.11	1.15	1.59	2.03	1.27	0.13	0.50	0.39	0.14	1.09	1.28	1.79	0.00	0.00	1.75	0.83	0.17	0.38	1.08	0.99	4.62	2.65
R8	0.27	0.92	0.57	0.76	0.97	0.00	0.00	0.05	0.09	0.00	0.09	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94	1.03	2.80	0.13
R9	1.68	3.04	0.96	1.05	1.10	0.00	0.00	0.29	0.94	0.33	2.23	1.00	2.15	0.46	0.44	0.00	0.30	2.13	0.54	0.13	0.11	1.09	1.17	5.63	4.38
R10	0.32	0.74	0.64	1.08	1.15	0.00	0.00	0.18	0.00	0.00	0.10	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.11	1.04	3.11	0.19
R11	0.32	0.62	0.14	0.93	0.80	0.00	0.00	0.23	1.74	1.67	1.88	1.00	1.24	0.62	0.00	0.00	0.00	0.08	0.00	0.00	0.00	1.00	1.03	2.53	6.03

**A 3. Centrality indices of the behaviors of the ethogram of Table 2 for the individuals of the Z-family (cf and cg were not shown).**

ID	gr	su	to	co	cr	di	ad	dw	th	gn	fi	ca	sn	fw	sc	sm	sw	pr	te	mo	cp	df	dr	sum_pos	sum_neg
<b>Z0</b>	0.44	0.69	0.40	0.89	0.90	1.21	0.33	2.78	0.33	0.00	0.00	0.25	0.74	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.87	1.09	3.15	4.86
<b>Z1</b>	0.71	1.93	1.81	1.03	1.05	0.89	2.28	1.09	1.00	0.83	1.39	0.50	1.17	0.94	1.24	1.83	2.37	1.29	2.10	1.39	2.74	0.87	1.04	7.78	8.65
<b>Z2</b>	1.28	1.94	3.12	1.45	1.13	0.43	0.33	0.49	3.10	1.83	1.72	1.64	2.27	3.75	3.09	0.00	1.22	4.52	1.20	0.73	0.69	0.95	1.04	7.95	7.99
<b>Z3</b>	1.92	0.79	1.85	1.21	0.87	0.09	0.00	0.91	0.83	1.00	0.97	0.33	2.62	3.10	0.63	0.00	0.20	1.81	3.63	0.33	0.13	1.05	1.07	4.29	3.60
<b>Z4</b>	1.01	0.07	0.17	0.82	1.02	0.00	0.50	0.22	0.13	0.00	1.00	1.00	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.92	2.69	0.50
<b>Z5</b>	1.84	0.34	0.10	0.72	1.38	0.11	0.00	0.05	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94	1.20	2.82	0.06
<b>Z6</b>	1.52	2.69	2.02	1.15	0.75	0.67	0.33	0.56	3.87	1.33	3.22	1.61	1.95	0.67	1.10	0.00	0.25	1.38	2.58	1.46	0.11	0.94	0.72	4.60	5.99
<b>Z7</b>	0.90	0.48	0.61	0.98	0.68	1.92	1.42	2.32	0.00	0.00	0.00	1.06	0.43	0.00	0.00	0.00	0.00	0.27	0.25	0.00	0.00	1.02	0.83	2.67	5.00
<b>Z8</b>	0.54	1.42	3.29	1.10	1.21	2.09	3.48	1.33	0.67	0.33	0.67	2.19	0.64	1.44	1.53	3.50	3.18	1.46	1.13	1.93	1.90	0.92	1.13	11.50	12.26
<b>Z9</b>	0.96	1.37	1.32	1.00	1.20	1.24	1.79	2.26	2.98	3.00	0.44	0.84	1.10	0.94	1.40	3.33	1.72	1.29	1.29	4.10	3.85	0.98	1.12	6.98	16.45
<b>Z10</b>	0.56	1.53	1.61	0.85	1.15	1.24	3.29	1.16	0.54	0.83	0.89	1.23	1.27	0.94	1.50	1.33	1.25	1.29	1.21	1.25	2.02	1.08	1.05	5.72	11.46
<b>Z11</b>	1.05	0.82	0.78	1.17	1.04	1.78	1.50	1.45	0.33	0.00	0.31	0.00	0.50	0.66	0.00	0.00	0.00	1.38	0.00	0.00	0.00	1.03	1.04	3.92	5.34
<b>Z12</b>	0.26	0.31	0.22	0.98	0.90	1.57	0.00	1.30	0.00	0.00	1.30	0.70	0.49	0.20	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.96	1.05	2.84	2.78
<b>Z13</b>	1.35	0.96	1.60	1.24	0.89	0.11	0.00	0.57	1.31	1.33	1.11	0.33	1.93	0.58	0.42	0.00	0.25	0.54	2.50	0.00	0.00	1.00	0.95	4.16	4.53
<b>Z14</b>	0.52	1.08	0.81	1.44	0.87	0.00	0.00	0.45	1.01	0.33	2.65	0.00	0.88	0.53	0.00	0.00	0.00	0.21	1.29	0.00	0.00	1.04	0.65	3.92	6.16

## Co-feeding tests - data

**A 4. Sum of the percentages of feeding- and proximity-related behaviors of all 12 trials.** Rows with “+” show dyads with an affiliative relationship, rows with “-“ show dyads with an agonistic relationship. Sex 1 – mixed-sex pairs, sex 2 – same-sex pairs.

Pair	sex	bl	dbl	mbi	cf	fa	fd
<b>B0+Z1</b>	1	280.90	78.92	735.09	104.90	1050.45	44.64
<b>B2+Z1</b>	2	173.95	201.34	798.58	24.08	1175.92	0.00
<b>B3+Z9</b>	1	44.33	74.31	1074.21	7.14	1192.86	0.00
<b>B6+B0</b>	2	188.17	212.07	799.76	0.00	1192.99	7.01
<b>B7+B12</b>	2	102.16	74.96	1009.06	15.13	1183.14	1.73
<b>B9+Z2</b>	2	260.15	158.95	738.41	45.49	1135.85	18.66
<b>B13+B1</b>	1	72.88	145.36	964.21	17.55	1182.45	0.00
<b>R11+R8</b>	2	391.20	115.43	476.76	220.69	970.81	8.50
<b>Z6+Z2</b>	2	588.90	142.97	376.66	90.62	1062.91	46.47
<b>Z8+Z11</b>	2	85.80	163.17	902.38	49.45	1146.15	4.40
<b>Z10+Z2</b>	1	768.36	188.42	221.03	23.29	1164.03	12.67
<b>Z11+Z1</b>	2	237.22	90.95	824.83	46.77	1149.78	3.45
<b>B0-Z4</b>	1	185.59	162.74	818.93	32.74	1167.26	0.00
<b>B2-R2</b>	2	191.54	253.47	742.76	12.48	1187.52	0.00
<b>B3-B12</b>	1	42.82	139.98	999.70	17.50	1182.50	0.00
<b>B6-R0</b>	2	404.12	120.93	617.33	57.62	1142.38	0.00
<b>B7-R9</b>	2	58.57	83.14	103.78	1066.00	1200.30	1136.02
<b>B9-Z12</b>	2	214.88	273.63	666.94	47.06	1131.23	21.72
<b>B13-R1</b>	1	73.82	86.45	1033.03	6.70	1185.27	8.04
<b>R11-B9</b>	2	26.63	22.25	1123.62	27.50	1172.50	0.00
<b>Z6-R0</b>	2	507.50	167.57	444.50	80.43	1113.90	5.67
<b>Z8-R9</b>	2	36.40	35.98	1120.50	56.60	1140.67	2.73
<b>Z10-B6</b>	1	366.27	225.57	544.72	69.61	1118.73	11.66
<b>Z11-Z10</b>	2	433.36	230.24	469.84	70.37	1118.77	10.86

**A 5. Frequency of feeding strategy, sociopositive and socionegative behaviors in all 12 trials for all the test dyads.** Rows with “+” show dyads with an affiliative relationship, rows with “-” show dyads with an agonistic relationship. Columns with “[1]” show data of the focal animals.

Pair	Di	Di [1]	Ad	Ad [1]	Dw	Dw [1]	Ag	Ag [1]	Sa	Sa [1]	sum_neg	sum_neg [1]	To	To [1]	Fp	Fp [1]
<b>B0+Z1</b>	0	0	0	0	3	0	3	0	6	0	6	0	0	0	12	6
<b>B0-Z4</b>	0	0	0	0	2	0	0	0	2	0	2	0	0	0	12	2
<b>B2+Z1</b>	0	0	0	0	2	0	1	0	3	0	3	0	1	1	12	2
<b>B2-R2</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	2
<b>B3+Z9</b>	0	0	3	0	3	0	0	0	3	0	6	0	0	0	12	0
<b>B3-B12</b>	0	0	0	0	1	0	0	0	1	0	1	0	0	0	11	1
<b>B6+B0</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0
<b>B6-R0</b>	0	0	0	0	3	0	0	0	3	0	3	0	1	1	12	0
<b>B7+B12</b>	0	0	1	1	11	0	6	1	17	1	18	2	0	0	12	6
<b>B7-R9</b>	0	0	0	0	7	0	1	0	8	0	8	0	0	0	12	0
<b>B9+Z2</b>	1	0	0	0	4	0	1	0	5	0	6	0	0	0	12	5
<b>B9-Z12</b>	0	0	1	1	16	16	2	2	18	18	19	19	0	0	12	12
<b>B13+B1</b>	0	0	0	0	1	1	0	0	1	1	1	1	1	0	12	12
<b>B13-R1</b>	0	0	0	0	4	4	0	0	4	4	4	4	0	0	12	12
<b>R11+R8</b>	0	0	1	1	10	7	3	2	13	9	14	10	0	0	12	6
<b>R11-B9</b>	0	0	0	0	6	1	2	2	8	3	8	3	0	0	12	2
<b>Z6+Z2</b>	0	0	0	0	6	0	5	3	11	3	11	3	4	4	12	1
<b>Z6-R0</b>	0	0	2	0	6	0	0	0	6	0	8	0	0	0	12	2
<b>Z8+Z11</b>	0	0	0	0	1	1	3	3	4	4	4	4	0	0	12	12
<b>Z8-R9</b>	0	0	0	0	3	3	4	4	7	7	7	7	0	0	12	12
<b>Z10+Z2</b>	1	0	3	0	4	0	2	0	6	0	10	0	2	2	12	4
<b>Z10-B6</b>	0	0	0	0	7	5	1	1	8	6	8	6	0	0	12	9
<b>Z11+Z1</b>	0	0	0	0	1	0	0	0	1	0	1	0	1	1	12	3
<b>Z11-Z10</b>	0	0	1	1	2	2	3	2	5	4	6	5	0	0	12	9



**A 6. Sum of the percentages of feeding- and proximity-related behaviors of mixed-sex dyads when females were in heat.** Rows with “+” show dyads with an affiliative relationship, rows with “-“ show dyads with an agonistic relationship.

<b>Pair</b>	<b>bl</b>	<b>dbl</b>	<b>mb1</b>	<b>cf</b>	<b>fa</b>	<b>fd</b>
<b>B0+Z1</b>	116.71	223.31	859.97	0.00	1200.00	0.00
<b>B3+Z9</b>	33.71	102.78	1063.51	0.00	1200.00	0.00
<b>B13+B1</b>	28.04	65.19	1106.77	0.00	1200.00	0.00
<b>Z10+Z2</b>	328.44	263.33	603.14	5.10	1194.90	0.00
<b>B0-Z4</b>	90.37	109.72	994.44	5.47	1194.53	0.00
<b>B3-B12</b>	57.41	157.29	969.90	15.40	1184.60	0.00
<b>B13-R1</b>	0.00	118.52	1081.48	0.00	1200.00	0.00
<b>Z10-B6</b>	103.68	39.40	1056.92	0.00	1189.97	10.03

**A 7. Frequency of feeding strategy, sociopositive and socionegative behaviors in all 12 trials for all mixed-sex dyads when females were in heat.** Rows with “+” show dyads with an affiliative relationship, rows with “-“ represent dyads with an agonistic relationship. Columns with “[1]” show data of the focal animals.

Pair	Di	Di [1]	Ad	Ad [1]	Dw	Dw [1]	Ag	Ag [1]	Sa	Sa [1]	sum_neg	sum_neg [1]	To	To [1]	Fp	Fp [1]
<b>B0+Z1</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0
<b>B0-Z4</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	1
<b>B3+Z9</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	12
<b>B3-B12</b>	1	1	0	0	1	1	0	0	1	1	2	2	1	0	12	10
<b>B13+B1</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	12
<b>B13-R1</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	12
<b>Z10+Z2</b>	0	0	1	0	1	0	2	0	3	0	4	0	0	0	12	1
<b>Z10-B6</b>	0	0	0	0	1	1	0	0	1	1	1	1	0	0	12	12

## Social network analysis - results

**A 8. Statistical results of the comparison between the three families: B, R and Z.** Test statistic of Kruskal-Wallis tests:  $N_B = 14$ ;  $N_R = 12$ ;  $N_Z = 15$ ;  $df = 2$ . Significant results are highlighted in bold type face. Post-hoc test – Dunn-Bonferroni test, bold type indicating that this family showed significantly more of the behavior in focus. There were no records of the behaviors co-feeding and chasing in group, so no statistical analysis could be conducted.

Behavior	Test statistic and level of significance	Post-hoc test	Post-hoc test
<b>Sociopositive</b>			
Greeting	$\chi^2 = 3.800$ ; $p > 0.05$		
Snuffling	$\chi^2 = 2.496$ ; $p > 0.05$		
Touching	$\chi^2 = 2.771$ ; $p > 0.05$		
Co-foraging	$\chi^2 = 3.703$ ; $p > 0.05$		
Co-resting	$\chi^2 = 0.012$ ; $p > 0.05$		
Sum of sociopositive	$\chi^2 = 5.457$ ; $p > 0.05$		
<b>Socioneegative</b>			
Displacement without body contact	$\chi^2 = 3.195$ ; $p > 0.05$		
Aggressive displacement without body contact	$\chi^2 = 1.840$ ; $p > 0.05$		
Displacement with body contact	$\chi^2 = 3.367$ ; $p > 0.05$		
Threatening	$\chi^2 = 1.165$ ; $p > 0.05$		
Gnashing of teeth (only males)	$\chi^2 = 1.841$ ; $p > 0.05$		
Fighting	$\chi^2 = 0.309$ ; $p > 0.05$		
Chasing alone	$\chi^2 = 4.771$ ; $p > 0.05$		
Sum of socioneegative	<b><math>\chi^2 = 6.544</math>; <math>p = 0.038</math></b>	<b>R – Z</b> $\chi^2 = -2.529$ ; $p = 0.011$	
<b>Mating-related</b>			
Sniffing	$\chi^2 = 0.978$ ; $p > 0.05$		
Following	$\chi^2 = 0.870$ ; $p > 0.05$		
Scenting	$\chi^2 = 3.239$ ; $p > 0.05$		
Scent marking (only males)	$\chi^2 = 5.241$ ; $p > 0.05$		
Scenting while another male is copulating	$\chi^2 = 4.893$ ; $p > 0.05$		
Prodding	$\chi^2 = 3.895$ ; $p > 0.05$		
Testing	$\chi^2 = 5.705$ ; $p > 0.05$		
Mounting	$\chi^2 = 3.616$ ; $p > 0.05$		
Copulating	$\chi^2 = 3.344$ ; $p > 0.05$		
<b>Grouping</b>			
Grouping during foraging	$\chi^2 = 3.867$ ; $p > 0.05$		
Grouping during resting	$\chi^2 = 0.188$ ; $p > 0.05$		

**A 9. Statistical results of the comparison between the three age classes: mother-sows (MS), litter1 (born in 2014) and litter2 (born in 2015).** Test statistic of Kruskal-Wallis tests:  $N_{MS}=3$ ;  $N_{Litter1}=18$ ;  $N_{Litter2}=20$ ;  $df= 2$ . Significant results are highlighted in bold type face. Post-hoc test – Dunn-Bonferroni test, bold type indicating that this age group showed significantly more of the behavior in focus. There were no records of the behaviors co-feeding and chasing in group, so no statistical analysis could be conducted.

Behavior	Test statistic and level of significance	Post-hoc test	Post-hoc test
<b>Sociopositive</b>			
Greeting	$\chi^2 = 4.157$ ; $p > 0.05$		
Snuffling	$\chi^2 = 1.073$ ; $p > 0.05$		
Touching	$\chi^2 = 1.827$ ; $p > 0.05$		
Co-foraging	$\chi^2 = 0.359$ ; $p > 0.05$		
Co-resting	$\chi^2 = 5.310$ ; $p > 0.05$		
Sum sociopositive	$\chi^2 = 1.387$ ; $p > 0.05$		
<b>Socionegative</b>			
Displacement without body contact	$\chi^2 = 3.548$ ; $p > 0.05$		
Aggressive displacement without body contact	$\chi^2 = 0.496$ ; $p > 0.05$		
Displacement with body contact	<b><math>\chi^2 = 6.217</math>; <math>p = 0.045</math></b>	<b>MS - litter1</b> $\chi^2 = -2.477$ $p = 0.013$	<b>MS - litter2</b> $\chi^2 = -1.994$ $p = 0.046$
Threatening	$\chi^2 = 0.285$ ; $p > 0.05$		
Gnashing of teeth (only males)	$\chi^2 = 0.432$ ; $p > 0.05$		
Fighting	$\chi^2 = 1.476$ ; $p > 0.05$		
Chasing alone	$\chi^2 = 0.697$ ; $p > 0.05$		
Sum socionegative	$\chi^2 = 3.568$ ; $p > 0.05$		
<b>Mating-related</b>			
Sniffing	$\chi^2 = 1.463$ ; $p > 0.05$		
Following	$\chi^2 = 4.291$ ; $p > 0.05$		
Scenting	$\chi^2 = 2.701$ ; $p > 0.05$		
Scent marking (only males)	$\chi^2 = 0.657$ ; $p > 0.05$		
Scenting while another male is copulating	$\chi^2 = 2.527$ ; $p > 0.05$		
Prodding	$\chi^2 = 0.035$ ; $p > 0.05$		
Testing	$\chi^2 = 2.980$ ; $p > 0.05$		
Mounting	$\chi^2 = 1.758$ ; $p > 0.05$		
Copulating	$\chi^2 = 1.603$ ; $p > 0.05$		
<b>Grouping</b>			
Grouping during foraging	<b><math>\chi^2 = 9.704</math>; <math>p = 0.008</math></b>	<b>MS - litter1</b> $\chi^2 = 2.222$ $p = 0.026$	<b>MS - litter2</b> $\chi^2 = 3.020$ $p = 0.003$
Grouping during resting	$\chi^2 = 0.525$ ; $p > 0.05$		

**A 10. Statistical results of the comparison of the behaviors of the mother-sows (MS) and their litters.** Test statistics of Mann-Whitney-U test:  $N_{MS} = 3$ ;  $N_{litters} = 38$ ; significant results in bold type face. There were no records of the behaviors “co-feeding” and “chasing in group”, so no statistical analysis could be conducted. As “gnashing of teeth” and “scent marking” are strictly male behaviors no tests were conducted.

Behavior	Test statistic and level of significance	Result
<b>Sociopositive</b>		
Greeting	$Z = -0.601$ ; $p > 0.05$	
Snuffling	$Z = 0.977$ ; $p > 0.05$	
Touching	$Z = 1.227$ ; $p > 0.05$	
Co-foraging	$Z = 0.576$ ; $p > 0.05$	
Co-resting	<b><math>Z = 2.179</math>; <math>p = 0.029</math></b>	MS showed less co-resting
Sum of sociopositive	$Z = -1.177$ ; $p > 0.05$	
<b>Socioneegative</b>		
Displacement without body contact	$Z = -1.638$ ; $p > 0.05$	
Aggressive displacement without body contact	$Z = 0.000$ ; $p > 0.05$	
Displacement with body contact	<b><math>Z = -2.303</math>; <math>p = 0.021</math></b>	MS showed more displacement with body contact
Threatening	$Z = -0.520$ ; $p > 0.05$	
Gnashing of teeth	Only male behavior	
Fighting	$Z = 0.902$ ; $p > 0.05$	
Chasing alone	$Z = -0.404$ ; $p > 0.05$	
Sum of socioneegative	$Z = -1.001$ ; $p > 0.05$	
<b>Mating-related</b>		
Sniffing	$Z = 1.001$ ; $p > 0.05$	
Following	<b><math>Z = 2.069</math>; <math>p = 0.039</math></b>	MS showed less following
Scenting	$Z = 1.366$ ; $p > 0.05$	
Scent marking	Only male behavior	
Scenting while another male is copulating	$Z = 1.306$ ; $p > 0.05$	
Prodding	$Z = 0.051$ ; $p > 0.05$	
Testing	$Z = 1.498$ ; $p > 0.05$	
Mounting	$Z = 1.182$ ; $p > 0.05$	
Copulating	$Z = 1.182$ ; $p > 0.05$	
<b>Grouping</b>		
Grouping during foraging	<b><math>Z = 2.735</math>; <math>p = 0.006</math></b>	MS showed less grouping during foraging
Grouping during resting	$Z = -0.550$ ; $p > 0.05$	

## Co-feeding tests – results

**A 11. Statistical results of the comparison of the influence of the relationship on the behavior in co-feeding tests of 12 dyads with an affiliative relationship and 12 dyads with an agonistic relationship.** Test statistics of Mann-Whitney-U test:  $N_{Af}=12$ ,  $N_{Ag}=12$ ,  $\alpha_a < 0.025$ .

	Behavior	Test statistic and level of significance
Sociopositive behavior	Touching	$Z = -1.547$ ; $p > 0.025$
Socionegative behaviors	Displacement without body contact	$Z = -1.446$ ; $p > 0.025$
	Aggressive displacement without body contact	$Z = -0.577$ ; $p > 0.025$
	Attempts of displacement	$Z = -0.671$ ; $p > 0.025$
	Displacement with body contact	$Z = -0.844$ ; $p > 0.025$
	Severe aggression	$Z = -0.609$ ; $p > 0.025$
Feeding strategy	First at the plate	$Z = -0.234$ ; $p > 0.025$
Feeding-related behaviors	Co-feeding	$Z = -0.635$ ; $p > 0.025$
	Feeding alone	$Z = -0.173$ ; $p > 0.025$
	Feeding next to the plate	$Z = -0.559$ ; $p > 0.025$
Proximity-related behaviors	Within body length	$Z = -0.751$ ; $p > 0.025$
	Within double body length	$Z = -0.520$ ; $p > 0.025$
	More than double body length	$Z = -0.115$ ; $p > 0.025$

**A 12. Statistical results of the comparison of the influence of the relationship on the behavior in co-feeding tests of the four mixed-sex dyads with an affiliative relationship and the four dyads with an agonistic relationship when females were in heat.** Test statistics of Mann-Whitney-U test:  $N_{Af}=4$ ,  $N_{Ag}=4$ ,  $\alpha_a < 0.025$ .

	Behavior	Test statistic and level of significance
Sociopositive behavior	Touching	$Z = -1.000$ ; $p > 0.025$
Socionegative behaviors	Displacement without body contact	$Z = -1.000$ ; $p > 0.025$
	Aggressive displacement without body contact	$Z = -1.000$ ; $p > 0.025$
	Attempts of displacement	$Z = -1.000$ ; $p > 0.025$
	Displacement with body contact	$Z = -0.683$ ; $p > 0.025$
	Severe aggression	$Z = -0.333$ ; $p > 0.025$
Feeding strategy	First at the plate	$Z = -0.464$ ; $p > 0.025$
Feeding-related behaviors	Co-feeding	$Z = -0.992$ ; $p > 0.025$
	Feeding alone	$Z = -1.692$ ; $p > 0.025$
	Feeding next to the plate	$Z = -1.000$ ; $p > 0.025$
Proximity-related behaviors	Within body length	$Z = -0.577$ ; $p > 0.025$
	Within double body length	$Z = -0.577$ ; $p > 0.025$
	More than double body length	$Z = -0.289$ ; $p > 0.025$

**A 13. Influence of heat on the behavior of mixed-sex dyads in co-feeding tests.** The column “affiliative” shows the statistical results of dyads with affiliative relationships when females were in heat compared to when they were not while the row “agonistic” shows the same for dyads with agonistic relationships. Significant results are highlighted in bold type face. Test statistics of Mann-Whitney-U test: affiliative:  $N_H=4$ ,  $N_{NH}=4$ ; agonistic:  $N_H=4$ ,  $N_{NH}=4$ ,  $\alpha_a < 0.025$ ; n.o. – not observed during the trials.

	Behavior	Test statistic and level of significance - affiliative	Test statistic and level of significance - agonistic
Sociopositive behavior	Touching	$Z = -1.512$ ; $p > 0.025$	$Z = -1.000$ ; $p > 0.025$
Socionegative behaviors	Displacement without body contact	$Z = -1.000$ ; $p > 0.025$	$Z = -1.000$ ; $p > 0.025$
	Aggressive displacement without body contact	$Z = -1.000$ ; $p > 0.025$	n.o.
	Attempts of displacement	$Z = -0.833$ ; $p > 0.025$	$Z = -1.000$ ; $p > 0.025$
	Displacement with body contact	<b><math>Z = -2.247</math>; <math>p = 0.025</math></b>	$Z = -2.084$ ; $p > 0.025$
	Severe aggression	$Z = -0.333$ ; $p > 0.025$	$Z = -2.084$ ; $p > 0.025$
Feeding strategy	First at the plate	$Z = -0.464$ ; $p > 0.025$	$Z = -0.744$ ; $p > 0.025$
Feeding-related behaviors	Co-feeding	<b><math>Z = -2.366</math>; <math>p = 0.018</math></b>	$Z = -2.033$ ; $p > 0.025$
	Feeding alone	<b><math>Z = -2.366</math>; <math>p = 0.018</math></b>	$Z = -2.021$ ; $p > 0.025$
	Feeding next to the plate	$Z = -1.512$ ; $p > 0.025$	$Z = -0.661$ ; $p > 0.025$
Proximity-related behaviors	Within body length	$Z = -0.866$ ; $p > 0.025$	$Z = -0.866$ ; $p > 0.025$
	Within double body length	$Z = -0.577$ ; $p > 0.025$	$Z = -1.155$ ; $p > 0.025$
	More than double body length	$Z = -0.577$ ; $p > 0.025$	$Z = -1.155$ ; $p > 0.025$



**A 14. Influence of sex of the test dyads on the behavior in co-feeding tests.** Comparison of mixed-sex dyads (Ms) and same-sex dyads (Ss). Test statistics of Mann-Whitney-U test:  $N_{Ms}=8$ ,  $N_{Ss}=16$ ,  $\alpha_a < 0.025$ .

	Behavior	Test statistic and level of significance
Sociopositive behavior	Touching	$Z = -0.425$ ; $p > 0.025$
Socionegative behaviors	Displacement without body contact	$Z = -0.244$ ; $p > 0.025$
	Aggressive displacement without body contact	$Z = -0.329$ ; $p > 0.025$
	Attempts of displacement	$Z = -1.497$ ; $p > 0.025$
	Displacement with body contact	$Z = -1.298$ ; $p > 0.025$
	Severe aggression	$Z = -1.588$ ; $p > 0.025$
Feeding strategy	First at the plate	$Z = -0.830$ ; $p > 0.025$
Feeding-related behaviors	Co-feeding	$Z = -1.408$ ; $p > 0.025$
	Feeding alone	$Z = -0.674$ ; $p > 0.025$
	Feeding next to the plate	$Z = -0.499$ ; $p > 0.025$
Proximity-related behaviors	Within body length	$Z = -0.612$ ; $p > 0.025$
	Within double body length	$Z = -0.428$ ; $p > 0.025$
	More than double body length	$Z = -0.857$ ; $p > 0.025$