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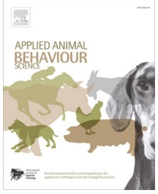

Social influence and attention bias in free-ranging domestic pigs: Effects of demonstrator rank and friendship

Ariane Veit [*], Isabelle Fuxjäger, Marianne Wondrak, Ludwig Huber

Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine Vienna, Medical University of Vienna, University of Vienna, Veterinaerplatz 1, Vienna 1210, Austria

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ABSTRACT

Pigs, as highly social animals, form stable hierarchies and different relationships to other members of their group. Pigs, mostly of very young ages, have been shown to use social learning to gather information about food locations and even extractive foraging techniques from various types of sources. The present study aims to investigate whether also adult pigs, living in a long-term stable kin-based sounder, use information of their group mates and, more specifically, whether this is based on their mates' rank or their relationship with them. The dominance order of 20 female semi-naturally housed Kune Kune pigs (aged between five to seven years) was established with dyadic hierarchy tests, where two pigs competed against each other over a monopolizable food source. Their affiliative relationships (i.e. friendships) towards each other were assessed based on observations during their daily lives. After finding suitable demonstrator dyads, differing in rank and/or relationship quality to the respective observer, six rounds of two-choice tests were conducted. Prior to each two-choice test, two demonstrators were positioned on each side of the observer and were allowed to feed from a trough with an assigned olfactory cue that provided additional information in the subsequent test. After two minutes, the observer pig was allowed to enter a test room and was given the choice between two food bowls, which were marked with the olfactory cues connected to the respective demonstrators. Results indicate that sows, irrespective of their own rank, preferred to pay attention to the relatively lower-ranking demonstrator during the exposure phase, possibly due to avoidance of the relatively higher-ranking demonstrator. Furthermore, the observers with higher sociability preferred to pay more attention to the demonstrators with whom they had better friendships. In the two-choice test, we found no significant effect of demonstrator rank or friendship. However, a left side bias in more sociable observers may point towards at least some social effects. Overall, the study provided evidence that not only dominance, but also socio-positive relationships between individuals affect the behaviour of domestic pigs.

1. Introduction

Social learning, i.e., the learning from others' actions or their products (Heyes, 1994; Huber, 2011a), can be accomplished through various mechanisms, from motivational ones like social facilitation and perceptual ones like stimulus or local enhancement, to more cognitively demanding processes like imitation or emulation (Galef and Laland, 2005; Huber, 2011a, 2007; Huber et al., 2009). While the latter implicates the act of learning by mimicking another individual (Whiten, 2000), the motivational and perceptual processes rather describe already known behavioural patterns being influenced or biased by social stimuli. These can be put under the umbrella term *social influence* (Whiten, 2000; Zentall, 2011). In foraging situations, social influence plays an important role in helping to navigate decisions on when, where, what and how to eat (Galef and Giraldeau, 2001). Observers can, for example, be socially influenced in their decision where to look for food, for example, through the presence of one or more conspecifics at a specific site, or via scent trails of previous foragers (Galef and Giraldeau, 2001). Indeed, olfaction can be a helpful guide to learn about food locations and palatability. For example, observers can be influenced to consume a certain diet after an interaction time with a demonstrator providing cues of a certain food (social enhancement of food

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[*] Correspondence to: Messerli Research Institute, Department of Interdisciplinary Life Sciences, University of Veterinary Medicine Vienna, Veterinaerplatz 1, Vienna 1210, Austria.

E-mail address: ariane.veit@vetmeduni.ac.at (A. Veit).

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preferences; Hoppitt and Laland, 2008). If this food has novel properties, like a novel smell or taste, food preferences may also be socially acquired via associative learning (e.g., observational conditioning of novel food; Zentall, 2011).

Whether socially provided information is taken up at all, depends on various factors, such as age, experience, conformity, kinship, or dominance (Huber, 2011b; Laland, 2004; Rendell et al., 2011). Individual differences in sociability, as well as social tolerance between individuals, are other key factors for the occurrence of social learning (van Boekholt et al., 2021). While more sociable individuals might get exposed to noteworthy behaviours of others more often, their relationship towards the demonstrator will impact how likely they are to be influenced by their observations, be it through facilitation or inhibition of exploration and learning (Hopper, 2021). Next to the hierarchy structure, and aside from mother-infant bonds, friendship is one of the building blocks of social tolerance (van Boekholt et al., 2021). Friendships between individuals are defined as regularly occurring socio-positive or affiliative interactions such as close proximity, social grooming or body contact (Massen et al., 2010).

As highly social animals, pigs are an interesting and even ethically relevant candidate to study the effects of friendship between observers and demonstrators on the occurrence of social learning. Studies have shown that pigs develop close bonds with other pigs (Goumon et al., 2020; Petersen et al., 1989). These close bonds are associated with co-resting between pairs of pigs (Durrell et al., 2004), social nosing (Camerlink and Turner, 2013) or auditory signals like a repeated grunt as greeting (Kiley, 1972). Various experiments have shown that after social interaction with conspecifics, pigs tend to eat the same flavoured food as their demonstrators (Figueroa et al., 2020b, 2013; Morgan et al., 2003, 2001; Oostindjer et al., 2011). Moreover, they showed observational learning when they watched a sibling find hidden food and followed its example by discovering the food in the same trough (Nicol and Pope, 1994). In their discussion, the authors raised the question whether the social status and identity of the demonstrator might have influenced the outcome (Nicol and Pope, 1994). Held et al. (2000) later found that dominant pigs would follow their knowledgeable subordinate conspecifics to food sources. However, whether also subordinate pigs would follow higher-ranking informed foragers was not investigated. Luna et al. (2021a) found that pigs would indeed pay more attention to dominant, compared to subordinate demonstrators. However, the presence of the dominant demonstrators would subsequently inhibit the observed behaviour during the test phase, whereas subordinate demonstrators would facilitate it (Luna et al., 2021a). The effect of relationship quality on the pigs' attention towards and learning from the demonstrator was so far only hinted at by Figueroa et al. (2013), as observers preferred the diet of familiar over unfamiliar conspecifics, likely due to closer snout to snout proximity of familiar demonstrators after they had consumed feed with a novel odour, compared to non-familiar demonstrators, whose whole body was explored instead. Whether pigs would show a preference for the information of certain individuals of an established social group based on their friendship remains unknown.

To close this knowledge gap, this study investigates the influence of friendship, in addition to the rank of the demonstrator, on the attention of an observer and whether this observation biases the subsequent choice of a feeding site in female domestic pigs, living in a long-term stable social group. Based on theoretical models ("copy friends", Laland, 2004), we predicted that pigs would pay more attention to, and would be more positively influenced by individuals towards whom they showed higher affiliation, compared to individuals towards whom they showed lower affiliation. Furthermore, we predicted that the effect of demonstrator rank on the pigs' behaviour would be similar to the findings by Luna et al. (2021a) with more attention directed towards more dominant demonstrators, and a subsequent negative influence of dominants in the two-choice task.

2. Methods

2.2. Animals and housing

Out of a mixed-sex group of 39 adult Kune Kune pigs (*Sus scrofa domesticus*), the 20 sows were tested, as in natural conditions pig sounders mostly consist of sows and their offspring. Thus, especially for female individuals, effects of relationship quality on social influence can be expected. The group of pigs lived in semi-natural conditions at the Haidlhof Research Station (Bad Vöslau, Austria) and were kept solely for the purposes of behavioural research. The group consisted of two (of originally three) sows of the same litter, born in 2013, and their offspring of two litters each, born on site in 2014 and 2015 (for more information see supplementary material (SM), Table S1). Pigs were never separated and therefore all knew each other from birth on. Since all pigs were always kept together, male offspring was vasectomised at five to six months of age, to prevent inbreeding but ensure natural behaviour. Female offspring had their natural cycle but were never bred with fertile boars, and therefore never had offspring themselves. At the time of testing, the sows were seven (N = 2), six (N = 9) and five (N = 9) years of age.

The pigs had 8 ha of pasture at their disposal, providing free access to fresh grass and herbs. Each afternoon, they were fed with boiled corn and pieces of fresh vegetables. The amount of feed was adjusted so that pigs stayed within a body condition score of 3 and 4. The pigs could find shelter in six insulated wooden huts (6 m^2), located in a 1 ha forest. Water was provided in two locations for drinking and in one location for wallowing, to enable cooling down and skin care.

2.3. Procedure

2.3.1. Friendship assessment

On a total of 43 days between June and mid-September 2020 scan and *ad libitum* videos were recorded of all 39 pigs with hand-held cameras. Per day, three scan recordings (morning, midday, and afternoon) of the whole enclosure (see SM, Figure S1) were executed, whereby each individual was recorded at least once, yielding 21 h 53 m of video footage. Additionally, *ad libitum* recordings captured any spontaneously displayed behaviour during the day, yielding 15 h 41 min of video footage. To capture the full range of behaviours and contexts, the afternoon feedings were recorded every two days via overhead network cameras, which yielded 37 days of feeding videos. Of each feeding, the first five minutes were coded, resulting in 3 h 10 min of video footage. Over the span of 76 days, data was collected on 59 days. For more information on the procedure of video recordings see SM.

Behavioural coding was done with the program Solomon Coder (beta version 19.08.02, © https://solomon.andraspeter.com). Observed behaviour was classified into affiliative, agonistic, and mating-related interactions, as well as mere proximity if no interaction was observed (for details on coded behaviours see SM, Table S2). Interobserver reliability was assessed via Fleiss' Kappa using the function kappam.fleiss of the package irr, version 0.84.1 (Gamer et al., 2019), in R, version 4.2.2 (R-Core-Team, 2022). For scan videos three raters had an agreement of $\kappa = 0.799$ on the observed interaction partner of an individual, and an agreement of $\kappa = 0.6$ on the observed interactions (based on 232 of 262 cases). For *ad libitum* videos two raters had an agreement of $\kappa = 0.852$ on the observed interaction partner of an individual, and an agreement of $\kappa = 0.884$ on the observed interactions (based on 330 of 446 cases). For feeding videos three raters had an agreement of $\kappa = 0.697$ on the observed interaction partner of an individual, and an agreement of $\kappa = 0.755$ on the observed interactions (based on 124 of 273 cases).

To calculate the friendship score of each individual with all the other individuals of this group, we first calculated the sum of all initiated affiliative and mating related interactions per individual of each dyad. Even though mating-related behaviour mainly occurred between different sexes, specific interactions (e.g. sniffing at the anogenital region) were also regularly observed within the same sex. Each individual of each dyad was assigned with its own sums of interactions, instead of merging interactions of both individuals of a dyad, to allow for a nuanced friendship assessment as the behaviour of each individual was considered. All sums were then adjusted for the total number of observations per individual to control for different observation times between individuals. The total number of observations for each individual consisted of all recorded initiated interactions, as well as instances in which no interaction was recorded during first sighting in scan and feeding videos. On average 8.6 ± 7.3 (mean ± SD) socio-positive interactions were recorded for female directed dyads, with a minimum of zero interactions for 40 of the 380 directed dyads (7 of the 190 undirected dyads) and a maximum of 35.8 interactions. Data for the female directed dyads were selected and z-transformed to a mean of zero and a standard deviation of one, resulting in the final friendship score.

2.3.2. *Rank assessment*

Agonistic interactions can provide insight into the social hierarchy, as higher-ranking individuals show more socio-negative behaviour (Knowles et al., 2004). However, our behavioural observations revealed a lack of socio-negative interactions between many of the female dyads. This might be in part due to the social organization being largely based on avoidance behaviour, rather than aggressive encounters (Hunter et al., 1988; Jensen and Wood-Gush, 1984). In order to assign each pig its rank in the group hierarchy, we therefore additionally executed dyadic hierarchy tests, in which two individuals competed against each other over a monopolizable food source, with the winner being dominant over the loser (David, 1987). Each female was tested with on average 8.1 other females, which had in previous dyadic hierarchy tests been identified as closest in rank. In total, 81 pairs were tested. Each of these pairs was tested in a minimum of three consecutive test trials. During the preparation of each test trial, a monopolizable food source (a hand full of boiled corn) was placed in a trough located in the centre of an 8 m x 8 m arena, while both pigs watched from different compartments. In their first test trial, they were let in simultaneously to compete over the food. In the second test trial, the “loser” had a head-start, giving her the possibility to reach the food source before her opponent. This procedure was repeated until one pig had monopolized the food three times. The winner of each pair was scored with one, the loser with zero. If neither of the two pigs could prevail over the other in four consecutive trials, both received 0.5 points. The results of the pairs that were not tested were either based on the behavioural observations ($N = 72$) or inferred by the results of the executed hierarchy tests ($N = 37$). The scores per pair were then used to calculate the David’s score (David, 1987) as a measure of dominance rank using the function getNormDS of the package steepness, version 0.3–0 (Leiva and de Vries, 2022), in R, version 4.2.2 (R-Core-Team, 2022). David’s scores (mean ± SD = 9.5 ± 2.91) were z-transformed to a mean of zero and a standard deviation of one.

2.3.3. *Two-choice test*

To test for the effect of demonstrator rank and friendship on the attention and decision-making of pigs, each of the 20 sows was presented simultaneously with two demonstrators differing in their rank and friendship score towards the observer. After two minutes of being exposed to the demonstrators feeding from a trough, observers were allowed to enter a test room and choose between two food bowls. We predicted that observers would be biased to walk towards the food bowl that was located on the side where the lower-ranking or more affiliative demonstrator was positioned during the exposure phase. In addition to this bias, we added the possibility for observers to associate the food bowls to the respective demonstrators by means of novel olfactory cues (see *Test environment*).

Each sow participated as observer in one test per week over six weeks, except for one pig who only took part in four tests. Each sow was additionally selected as demonstrator, on average 11.8 times (SD = 1.28). In total, 118 tests were conducted, each with a unique triad combination of observer and demonstrators. Of these 118 tests, 84 were conducted with unique demonstrator dyads. In the remaining 34 tests, 17 demonstrator dyads were used for two different observers. In these cases, rank differences between demonstrators were the same, but friendship scores differed. Each observer encountered each of the selected demonstrators only once.

Per observer, six demonstrator pairs were selected differing in friendship along the whole range of ranks, as well as differing in rank along the whole range of friendship scores. In total, we had selected 28 demonstrator pairs of similar rank and friendship (both scores within 1 SD of each other), 22 demonstrator pairs of different rank and friendship (both scores differed more than 1 SD), as well as 34 demonstrator pairs of similar rank and different friendship, and 34 demonstrator pairs of different rank and similar friendship (see SM, Figure S2). On average, 6.6 high-ranking and 5.2 low-ranking demonstrators were selected per observer, as well as on average 6.7 demonstrators with high and 5.1 with low friendship scores (high and low refers to above and below average of the whole group of females). This selection procedure revealed no significant bias regarding an interaction of demonstrator rank and friendship scores (for more details on the relation of demonstrator rank and friendship see SM).

2.3.3.1. Test environment. The tests took place in a 5.5 m x 5.5 m test room in a purpose-built wooden test house with three adjacent outdoor compartments (each 1.8 m x 1.8 m) and a waiting area (5.4 m x 1.8 m), separated by a metal fence (Fig. 1). The observer was positioned in the middle outdoor compartment, while the demonstrators occupied the two compartments on the left and right side. In each of the two demonstrator compartments, one food trough was placed in the middle of the fence adjacent to the observer compartment, so the demonstrators were facing the observer while eating. The observers could thereby get close enough to perceive olfactory cues applied to the demonstrators’ foreheads. Prior to testing, each pig had been randomly assigned with a different unfamiliar aroma (ordered at https://www.ellisaromen.de/; see SM, Table S4). Ten drops of every aroma were diluted in 100 ml tap water and filled up in spray bottles, before being sprayed on the demonstrator pigs’ forehead.

The observer’s entrance to the test room was blocked by an opaque guillotine door, until the experimenter opened it from the inside of the room. The experimenter was positioned centrally in the back of the test room, hidden behind a wooden cover. Two food bowls, covered with slim wooden lids, were positioned on both sides of the room in equidistance (2.80 m) from the guillotine door. Each food bowl was filled with one soup ladle scoop of non-aromatised soaked wheat bran formed into a ball. To provide the olfactory guidance, two aroma-tainted cloth strips were wall-mounted at a height of 50 cm and lead from the observer’s entrance to each of the two food bowls. The cloth strips were first soaked in water, after which a few drops of the pure aroma were added every 10 cm. Before each usage, the cloth strips were re-tainted with the respective aroma to ensure non-degrading aroma intensity. The aromas always matched the side of the demonstrators’ position.

To habituate the pigs to the (then new) testing environment, all pigs could explore the empty room individually during two weeks prior to testing. If they did not dare to enter the room in the first instance, they were provided with other opportunities the following days until every individual had successfully and voluntarily accessed the room. Thereupon, every female was fed three consecutive times in the middle of the room, and also in the two demonstrator compartments, with soaked wheat bran.

2.3.3.2. Test procedure. Once the demonstrator pigs were positioned in the left and right outdoor compartments and were feeding on dry wheat bran, the assigned olfactory cues were sprayed on the demonstrators’ forehead. The observer pig was then led into the middle compartment

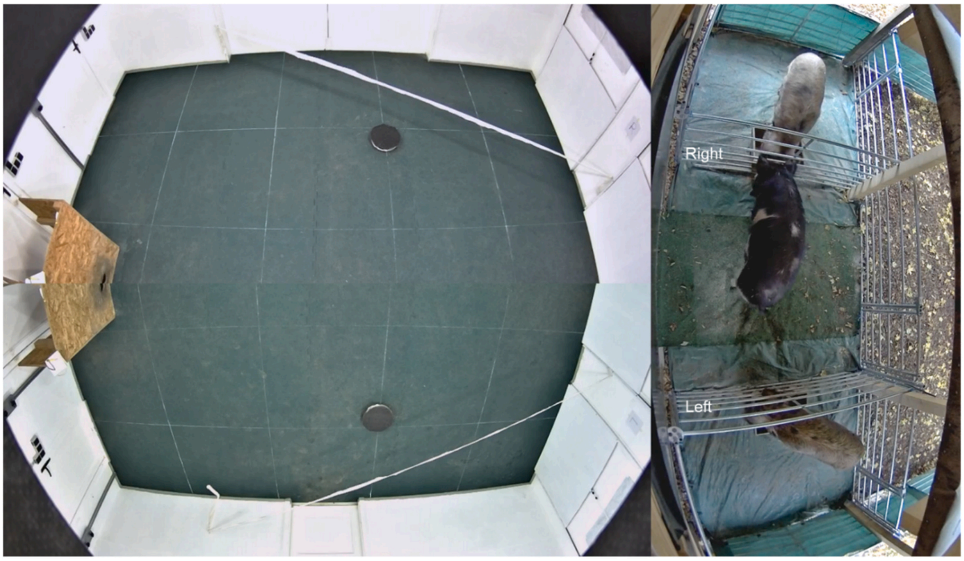

Fig. 1. Image of the test room and the adjacent outdoor compartments.

where she could observe and interact with the two demonstrators for two minutes. When the exposure phase ended, the experimenter opened the guillotine door and once the pig was inside the test room immediately closed it again. This marked the beginning of the test phase. Once the pig had started to lift the lid of one food bowl with its snout it was considered a choice and the experimenter removed the other food bowl, so the pig could only retrieve one food reward. After each test, the test room was aired with all eight doors open for at least 15 min before starting a new test.

To counteract a possibly developing side bias by choosing a bowl in the test room, every tested pig was, after a few hours, once again led to the test room. This time no demonstrators were present, and no cloth strips were installed. Both food bowls were positioned as in the test, with only the food bowl of the previously rejected side being filled with soaked wheat bran. If the pig chose again the same side it chose in the actual test, it was led out into the observer compartment and was given another possibility to choose again. This procedure was repeated until the pig had chosen the baited food bowl, with a maximum of 10 trials. After successfully choosing the other side, the pig had to re-enter the room two more times while one food bowl was placed in the middle of the room, to centre the last positive experience. Pigs therefore received per day one reward on the left, and one on the right side of the room, with two final rewards in the middle of the room. One week later, the next test was executed. Since all subjects acted both as observer and demonstrator, it was necessary to also prevent side bias development during demonstrations. Even though each demonstrator was positioned left or right in a counterbalanced manner, with on average 49.96% of trials per pig on the left (SD = 9.97%), their position as demonstrator on a given day could have impacted their subsequent choice as an observer. The demonstrators were therefore given the possibility to gain experience in both demonstrator compartments on a given test day, by switching places after the test and once again being fed with soaked wheat bran.

2.3.3.3. Data collection. While one network camera (AXIS M3065-V) recorded the outside compartments during the exposure phase, two overlapping network cameras (AXIS M3045-WV) captured the pig's choice in the test room. All three videos were combined and recorded using OBS Studio (version 26.1.1, © https://obsproject.com). To code the behaviour during the time the observer spent watching a demonstrator, Solomon Coder (beta version 19.08.02, © https://solomon.andraspeter.com) was used. The exposure phase started as soon as the observer entered her compartment and ended when she left through the guillotine door. The pig was considered to pay attention to one specific demonstrator once her head was directed towards the left or right demonstrator compartment. If the observer's head direction crossed the outside edge of the demonstrator compartment, it was encoded as a non-observing position. Additionally, we coded the proximity of observers to the respective demonstrators whenever the observers' head was positioned within 40 cm range to the left or right demonstrator compartment (i.e. whenever the nose of the observer was by crossing the carpet-tarp line, see Fig. 1). The bowl choice was recorded by the experimenter during testing. Interobserver reliability for coding head direction and position was assessed via intraclass correlation coefficients using the function icc of the package irr, version 0.84.1 (Gamer et al., 2019), in R, version 4.2.2 (R-Core-Team, 2022). Two raters coded 12 videos (10%) and had an agreement of on average 0.99 ± 0.01 (mean ICC ± SD) for duration of left and right head direction and head position, as well as total exposure phase duration.

2.3.4. *Data analysis*

First, we compared the attention and proximity variables collected during the exposure phase (i.e. proportion of duration of head directed to left compared to right demonstrator, and proportion of duration of being within 40 cm of left compared to right demonstrator compartment), by means of a Pearson's product-moment correlation, to establish whether both variables would serve as independent indicators for attention and proximity. However, since both were highly correlated (see results), we proceeded with analysing only the attention variable.

To investigate, whether demonstrator rank or friendship had an effect on the attention of the observers towards the demonstrators, a beta regression model was fitted using as dependent variable the proportion of observation time towards the left (compared to the right) demonstrator compartment. To investigate the effect of demonstrator rank or friendship on the observer's bowl choice, a generalized linear mixed model with binomial error structure was fitted, using as dependent variable the observer's bowl choice (right = 0, left = 1). In both models, the differences between demonstrator ranks and friendship scores were used as fixed effects. Both values were calculated by subtracting the right demonstrator's values from the left demonstrator's values. Positive values thereby indicate a greater rank or friendship of the left demonstrator compared to the right, whereas negative values indicate a greater rank or friendship of the right demonstrator. Since also observer traits like rank and sociability might interplay with this effect, we used two-way interactions between demonstrator rank difference and observer rank, as well as demonstrator friendship difference and observer sociability as test predictors. Observer sociability was calculated by taking the mean friendship score of each observer to all other females in the group. This value was equivalent to the amount of initiated affiliative interactions of each observer, adjusted for the respective total number of observations. Test number was included as control variable and was, like observer sociability, z-transformed to a mean of zero and a standard deviation of one, before including it into the model to ease model interpretation and model convergence (Schielzeth, 2010). Observer ID was included as random intercept with demonstrator rank difference, demonstrator friendship difference and test number as random slopes. The interaction between these random slopes and intercept was removed from the generalized linear mixed model since absolute correlation parameters were estimated as 1, being in part unidentifiable (Matuschek et al., 2017). This led only to a minor reduction in model fit (log-likelihoods, model with correlation parameters included: −75.313, df = 18; model without correlation parameters: −76.816, df = 12). The interaction between the random slopes and intercept was also removed from the beta regression model, as model complexity would otherwise prevent model convergence. Models were fitted in R, version 4.2.2 (R-Core-Team, 2022), using the function glmer of the package lme4, version 1.1–31 (Bates et al., 2015), and the function glmmTMB of the package glmmTMB, version 1.1.7 (Brooks et al., 2017).

After fitting the full model, we confirmed that none of the model assumptions were violated. We verified absence of collinearity by calculating the Variance Inflation Factor for the simple linear regression models without interactions and random effects structure (maximum VIF = 1.053). We furthermore found no overdispersion of the response of the beta regression model (dispersion parameter = 1.127). Finally, we evaluated model stabilities by dropping the individuals from the data one at a time and compared the estimates for these models with those obtained for the full data set. For this purpose, we used a function kindly provided by Roger Mundry. This revealed the models to be of good stability (see SM, Tables S5 and S6).

To test the overall effect of the fixed effects of interest (demonstrator rank difference in an interaction with observer rank, demonstrator friendship difference in an interaction with observer sociability), we compared the full model with all terms included to a null model lacking these predictors of interest (Forstmeier and Schielzeth, 2011), using a likelihood ratio test by setting the argument ‘test’ of the function anova of the package stats, version 4.2.2 (R-Core-Team, 2022), to “Chisq” (Dobson, 2002). Fixed effects were then individually tested by dropping them from the model one at a time, and comparing the simpler with the more complex model using likelihood ratio tests by setting the argument ‘test’ of the R function drop1 of the package stats, version 4.2.2 (R-Core-Team, 2022), to “Chisq” (Barr et al., 2013). To estimate confidence intervals for model estimates, we bootstrapped model estimates using the function bootMer of the package lme4, version 1.1–31 (Bates et al., 2015). Model results were plotted using the plot_model function of the package sjPlot, version 2.8.15 (Lüdecke, 2023).

3. Results

3.1. Attention

Of the two-minutes exposure phase, observers paid on average 50.9% attention towards the demonstrators and were on average 47.2% of the time within 40 cm range of a demonstrator compartment. The observers’ attention correlated with their position within the compartment (Pearson’s product-moment correlation: $r = 0.948$, $t_{(116)} = 32.126$, $P < 0.001$), meaning the duration they directed their heads towards the left or right demonstrator closely matched the duration of being within 40 cm range of the respective demonstrator compartment. The observers’ attention even increased over the number of trials from 45.6% in trial 1–59.3% in trial 6.

With regard to the predictors of interest, we found a significant effect of the interaction of demonstrator friendship and observer sociability, as well as demonstrator rank on the observers’ attention towards the two demonstrators ($\chi^2_{(6)} = 20.039$, $P = 0.003$). Observers with average and above average sociability scores thereby preferred to pay attention to the more affiliated demonstrator, whereas less sociable observers paid more attention to the less affiliated demonstrators ($\chi^2_{(1)} = 4.425$, $P = 0.035$, Fig. 2A). Irrespective of their own rank, observers furthermore paid more attention towards the demonstrator with lower rank ($\chi^2_{(1)} = 6.666$, $P = 0.01$, Fig. 2B). For model results see SM, Table S5.

3.2. Choice

The full null model comparison for the observers’ decision in the two-choice test revealed no significant effect of the predictors of interest ($\chi^2_{(6)} = 8.518$, $P = 0.203$). Therefore, neither demonstrator rank nor the friendship towards the demonstrators significantly influenced the observers’ food bowl choice (for model results see SM, Table S6; Fig. 3). Albeit not significant, model results did indicate a side bias effect, with the probability of choosing the left over the right food bowl increasing with higher observer sociability (Table S6; Fig. 4). Upon closer inspection, we found that of the six most sociable observers, four chose left in at least five out of six trials (Fig. 4, dots above the 75% mark), whereas two observers with below average sociability chose right in at least five out of six trials (Fig. 4, dots below the 25% mark).

4. Discussion

Attention to and using information from others can be biased due to the social organization of a group, with certain individuals being more likely to be observed due to their proximity to others (i.e. social tolerance, van Schaik, 2009), mediated for example by their rank or their social relationships (directed social learning, Coussi-Korbel and Fragaszy, 1995). In this study we investigated, which effect demonstrator rank and friendship might have on the attention and decision making of free-ranging domestic pigs. We exposed 20 female Kune Kune pigs to two demonstrators simultaneously, differing in rank and friendship towards the observer, and subsequently tested them in a two-choice test (with the aid of olfactory cues) to establish whether observers were socially influenced by the demonstrators.

Like predicted, the better the friendship between observer and demonstrator, the more an observer paid attention to the respective demonstrator. However, this was dependent on the observers’ sociability, as observers with higher sociability scores paid more attention to their friends than less sociable observers. Sociability in this study was measured by using the average friendship scores to all other females of the group, which was equivalent to the amount of initiated affiliative interactions. This measure might not only be a proxy for sociability, but also by extension for social competence, as social competence can be fostered by more social experience (Taborsky, 2021). Social competence usually leads to more appropriate social behaviour during socio-negative encounters, but can also increase social tolerance and foster social bonds (Taborsky, 2021). It is therefore possible that pigs with higher social competence preferred to attend to their friends, whereas individuals with low social competence were less focussed on this aspect of the demonstrator identity.

In potentially competitive situations, and especially if space to retreat is limited, dominance plays an important role in mediating social tolerance. Indeed, we found that also demonstrator rank impacted the attention towards the demonstrators. Lower-ranking demonstrators were attended to for longer, even irrespective of the observers’ own rank. This finding stands in contrast to many studies reporting higher attention towards dominant over subordinate individuals (chimpanzees: Kendal et al., 2015, pigs: Luna et al., 2021a, 2021b, horses: Krueger and Heinze, 2008, laying hens: Nicol and Pope, 1999). It is believed that the adaptive value for this attendance bias towards dominants is due to their access to valuable resources, previously demonstrated knowledge and

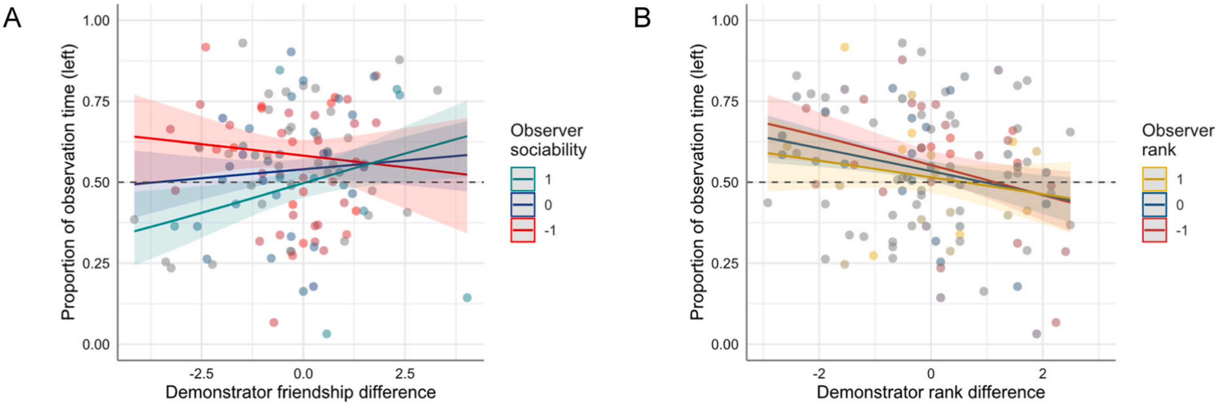

Fig. 2. Proportion of observation time of left (versus right) demonstrator, plotted for effects of A: demonstrator friendship difference in interaction with observer sociability, and B: demonstrator rank difference. Observer sociability is a continuous variable. Model regression lines including confidence intervals are given for observer sociability and observer rank being at their mean (i.e., 0), and at the mean ± SD (i.e., 1 and −1). Both, demonstrator rank and demonstrator friendship differences indicate a relative affiliation value for the left (versus the right) demonstrator. Thus, a decreasing slope across the 50% mark indicates preference for lower-ranking/less affiliated demonstrators, whereas an increasing slope indicates a preference for higher-ranking/more affiliated demonstrators.

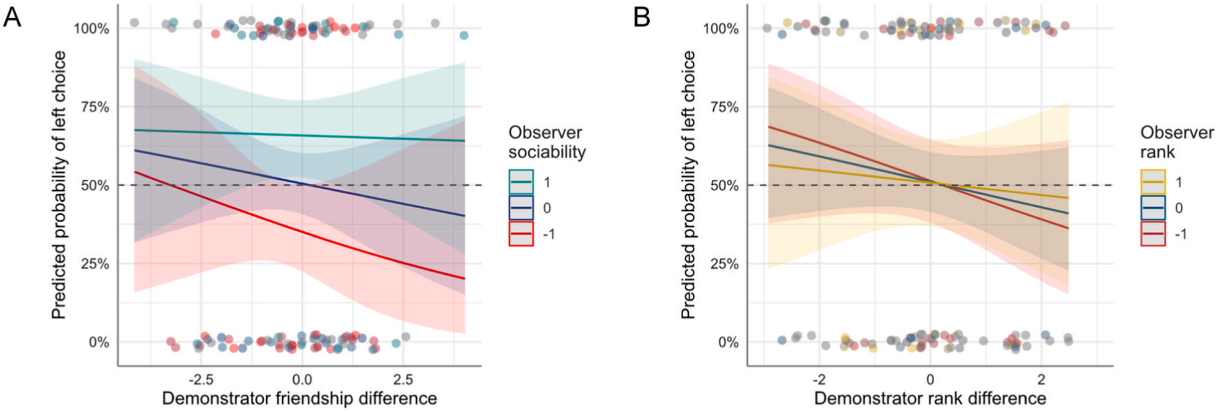

Fig. 3. Predicted probability to choose the left (versus right) food bowl, plotted for effects of A: demonstrator friendship difference in interaction with observer sociability, and B: demonstrator rank difference in interaction with observer rank. Model regression lines including 95% confidence intervals are given for observer sociability and observer rank being at their mean (i.e., 0), and at the mean ± SD (i.e., 1 and −1). Predicted probabilities above the 50% mark may indicate a preference for the left food bowl, whereas probabilities below the 50% mark may indicate a preference for the right food bowl. Both, demonstrator rank and demonstrator friendship differences indicate a relative affiliation value for the left (versus the right) demonstrator. Thus, a decreasing slope across the 50% mark may indicate a preference for lower-ranking/less affiliated demonstrators. The full null model comparison for this model was not significant.

success (Kendal et al., 2015). However, the effect of dominance is also affected by other variables, such as spatial distance between demonstrators and observers. Since the observer in this study was positioned between both demonstrators with only little room to retreat, which in contrast was possible in their 8 ha enclosure during daily life activities, observers might have been more cautious to direct their heads towards the more dominant demonstrators, let alone come within 40 cm range. Pigs have been suggested to live in a social organization largely based on avoidance behaviour, rather than direct aggression (Hunter et al., 1988; Jensen and Wood-Gush, 1984). It is therefore possible that dominant demonstrators had an inhibiting effect, rather than lower-ranking demonstrators eliciting an inherent attendance bias. However, we would expect to see an effect of the observer's own rank in this case, since lower-ranking observers should exhibit stronger avoidance behaviour than higher-ranking individuals. This effect was negligible in this study.

It is important to note that the two demonstrator traits (rank and friendship) were not significantly related. It is therefore unlikely that one finding was determined (i.e., confounded) by the other. This also suggests that observers with high sociability preferred the more affiliated demonstrator over the other, even if she was higher-ranking. The inhibitory effect of dominance on social tolerance therefore could have been mitigated by the friendship between individuals, particularly for more sociable or socially competent observers.

Contrary to our expectations, the pigs in this study did not show an effect of social influence by the demonstrator on their subsequent decision in the two-choice task. Social learning has been found in pigs in several studies (Luna et al., 2021b, 2021a; Nicol and Pope, 1994; Veit et al., 2017), in particular with regard to food preferences (Figueroa et al., 2021, 2020a, 2020b, 2013; Morgan et al., 2003, 2001; Oostindjer et al., 2011). However, recently we could provide evidence that adult pigs likely prefer to learn via non-social cues (through emulation), and that in some cases, conspecific demonstrators might have an inhibiting rather than enhancing effect, even if out of sight (Veit et al., 2023). In this study, too, we investigated the topic of social learning (more specifically, social influence) in adult pigs. It is possible that, like in many other species, social learning in pigs is mostly used by young animals (Voelkl et al., 2006), and the likelihood of social learning occurring decreases over time (Mesoudi et al., 2016; Schiel and Huber, 2006; but see Penndorf and Aplin, 2020). However, in this experiment we used a simple two choice task, which did not necessitate associative learning, but rather relied on simple biasing effects. While pigs were provided with additional olfactory cues which they could have used to associate the bowls to the respective demonstrators in each trial, no associative

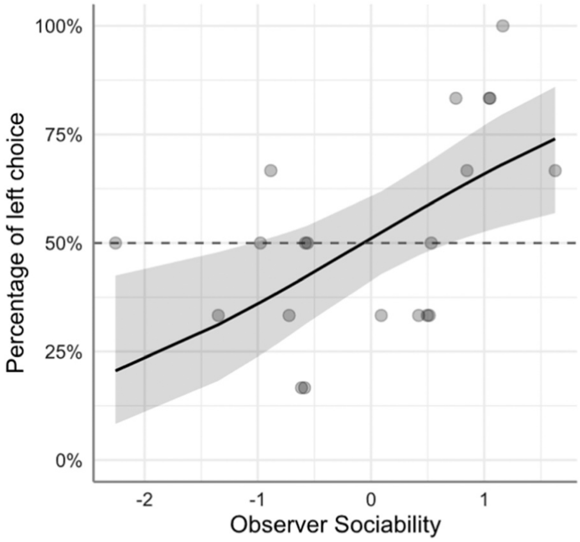

Fig. 4. Percentage of trials in which the left food bowl was chosen, for each observer, indicated by their respective sociability score. The model regression line of the predicted probability to choose the left (versus right) food bowl for the effect of observer sociability is given with a 95% confidence interval. The full null model comparison for this model was not significant.

learning was necessary in order to alter their behaviour. Rather, pigs were expected to be biased (socially influenced) by certain demonstrators in their foraging decisions, i.e. going to the left food bowl, if the more dominant or less affiliated demonstrator was positioned on the right side.

While some of these bowl choices might even have been biased in this way, it is possible that other bowl choices were made based on factors such as aroma preferences or simple side biases. For example, previously it was shown that pigs may exhibit differences in investigative behaviour when presented with different olfactory cues (Rørvang et al., 2023). Therefore, in the present study, the different olfactory cues that were assigned to each demonstrator might have also triggered a certain preference, which could have overshadowed the social influence of the respective demonstrators (Galef and Whiskin, 1998).

Additionally, we found that some individuals preferred the left (N = 4) or right (N = 2) food bowl, even though we had taken multiple countermeasures to avoid side biases. Model results indicated that this side bias might be related to the sociability of the observer. Observers with higher sociability thereby showed an increased likelihood to choose left. Research has shown that perceptual biases and asymmetrical motor responses are subject to the hemispheric specialization of the vertebrate brain (Rogers, 2023). While the left hemisphere (right eye) attends to familiar and more positively connotated stimuli, the right hemisphere (left eye) rather attends to unexpected stimuli and controls the expression of strong emotions, including fear and aggression (Leliveld et al., 2013; Rogers et al., 2013). The right hemisphere is also used in social behaviour (Rogers, 2021; Salva et al., 2012; Siniscalchi et al., 2021), which can involve dominance and aggression (Austin and Rogers, 2012) but also affiliative interactions (Farmer et al., 2018). Observer pigs with higher sociability therefore might have shown a bias towards the left food bowl due to their increased emotional arousal elicited by the preceding exposure phase. While this interpretation may seem fitting, no definitive conclusions should be drawn, since the full null model comparison for the food bowl choice was not significant.

Overall, this study provides evidence of an attention bias in favour of lower-ranking demonstrators, likely due to close proximity during the exposure phase. The inhibiting effect of dominance on attention might have been mitigated in part by a combination of friendship and social competence on behalf of the observers, since more sociable observers directed their attention also to the more affiliated demonstrators. In the two-choice test, observers did not seem to be socially influenced by the demonstrators' rank or friendship in choosing a food bowl. While food bowl choices might have been made based on various factors, results indicated that observers with higher sociability were more likely to exhibit a left bias in the two-choice test. This laterality effect might have been a result of a stronger emotional response of the more sociable sows to the exposure phase. In conclusion, the attention and decision making of pigs, particularly while in proximity to conspecifics, is indeed influenced by social factors, such as observer-demonstrator friendship, demonstrator dominance, as well as observer sociability. Social competence may be of particular importance in these situations, especially if space is limited and the context is perceived as competitive, e.g. in food-related tasks. The pigs of this study likely benefitted from a lifelong stable herd structure in a semi-natural environment, enabling them to foster close social bonds and develop social competences. Future studies on social relationships in pigs could also take male group members into account and identify possible differences between males and females in how their relationships may influence each other's behaviour. In general, research on farmed animals should increase their attention to animals housed in close to natural conditions, to provide adequate representation of their relationships, social dynamics, and socio-cognitive abilities.

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Ethical statement

The study is discussed and approved by the institutional ethics and animal welfare committee of the University of Veterinary Medicine Vienna (reference number ETK-168/11/2020), in accordance with good scientific practice guidelines (The European Code of Conduct for Research Integrity, Strasbourg 2011) and Austrian national legislation. All pigs have been trained to respond to their individual names when called and were highly motivated by occasional food rewards to follow the experimenters and participate in the tests (positive reinforcement only).

CRediT authorship contribution statement

Ariane Veit: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft. **Isabelle Fuxjäger:** Data curation, Investigation, Methodology, Writing – original draft. **Marianne Wondrak:** Conceptualization, Methodology, Supervision. **Ludwig Huber:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2024.106285.

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