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Demonstrator-dependent choice via olfactory cues in a stable sounder of free-ranging Kune Kune pigs (*Sus scrofa domesticus*)

Diploma Thesis

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Table of Content

1 Introduction

1.1 Social learning strategies

Living in groups brings many advantages for animals, such as a decreased chance of predation or an increased foraging success (Rubenstein 1978). Particularly, as social learning has proven to be a method requiring little costs to acquire new information (Rendell et al. 2011). Social learners are information “scroungers” by copying the behaviour of “producers” who spend energetic costs for sampling the environment (Barnard and Sibly 1981). The “scroungers” save themselves the trouble of generating information, which results in achieving a level of higher fitness compared to asocial learners but only if there are fewer “scroungers” than “producers” (Laland 2004). When the number of copiers increases, fewer individuals explore their surroundings, the information becomes less dependable and therefore the advantage concerning fitness will decrease (Rogers 1988). Eventually, the population will overcome a point of equal fitness (Barnard and Sibly 1981). As a result, the individuals have to decide under which occasion and from which individual they should copy, referred to as “when” and “who” strategies (Laland 2004).

Laland (2004) described three “when” strategies: The individuals copy “when uncertain”, “when asocial learning is costly” and finally “when the established behaviour is unproductive” (Laland 2004). Galef and colleagues (2008) tested one “when” strategy with Norway rats (*Rattus norvegicus*), giving the observer the choice between two differently flavoured unknown diets, while one diet was consumed by a demonstrator. By testing the motivation underlying copying “when uncertain”, the rats were taught that consuming unfamiliar food would result in illness induced by a toxicosis. When placed in an unfamiliar environment, these rats would follow their demonstrators’ example by tasting new food (Galef et al. 2008).

Laland (2004) also described various “who” strategies: For example “copy older individuals”, “copy if dissatisfied” or “copy friends” (Laland 2004). Krueger and colleagues (2014) concentrated on the “copy older individuals” approach: Observer horses *(Equus caballus)* watched a demonstrator horse opening a box containing food. Low-ranking horses chose to learn from older (thus high-ranking) horses in their group (Krueger et al. 2014). Similar findings can be reported with chimpanzees (*Pan troglodytes)*, as they preferred to watch dominant individuals over subordinates opening a feeding box by sliding a door. It is believed that dominants are more frequently copied due to their access of valuable resources, previously demonstrated knowledge and success, referred to as attendance bias (Kendal et al. 2015). Generally, a dominant individual is respected more highly and receives more attention, be it at grooming (Mishra et al. 2020, Schino 2001), or when selected as an ally out of an audience during a conflict (Kajokaite et al. 2019), or when sharing food (Massen et al. 2011).

A possible divergence from this rule might be the fact that individuals with stronger social bonds might be more tolerant of each other and could thereby not deal as much with monopolization due to rank difference. Also Laland (2004) proposed that animals should copy friends more often than non-affiliates (Laland 2004). This is confirmed by a study of Scheid and colleagues (2007) on ravens (*Corvus corax)*. The ravens were split into dyads, so each raven had either a demonstrator with a close affiliate relation or without affiliate relation. The observer could watch the demonstrator performing an object manipulation task and foraging task through a small hole, while the observation time was measured, as well as the activity of the demonstrator. Results showed that the observer spent more time watching affiliates than non-affiliates (Scheid et al. 2007). Another study with jackdaws (*Corvus monedula)* reached a completely different result: The jackdaws preferred to rather watch non-affiliates than affiliates manipulating an object (Schwab et al. 2008). The authors explained this result with the fact that jackdaws spend most of their time in close proximity to their partner, so they both experience the same feeding situations. In order to gain new information, they therefore orient themselves towards non-affiliative and thus spatially more distant individuals.

Due to their monogamistic lifestyle, the jackdaws did not behave as generally assumed. In contrast, in most group living animals, the role model for copying actions is believed to be an affiliative conspecific, rather than an individual with whom they have an agonistic relationship. Perry (2011) argued that individuals with close bonds will behave similarly due to an inherent desire, as was found in capuchin monkeys (Genus *Cebus*) (Perry 2011). This desire to behave similarly can ultimately lead to a conformity effect, in which individuals of one group will all adopt the same behaviour, even if initially different solutions were present (Morgan and Laland 2012).

1.2 Social influence on behaviour

Social learning can be accomplished through various mechanisms, that are either on a motivational or perceptual level, like social facilitation or enhancement, or they can be accomplished by using more cognitively demanding processes, like imitation or emulation (Galef 2013, Galef and Laland 2005, Range et al. 2007) . While in the former already known behaviour-patterns are influenced by conspecifics (social influence), in the latter the final outcome is learning a new behaviour. Therefore, in comparison to more complex social learning mechanisms, social influence does not implicate the act of learning by mimicking another individual (Whiten 2000). Furthermore, according to Nicol (1995), social influence can only be described as social learning, if the observer's behaviour changed even though the initial cue is absent (Nicol 1995).

For example young sika deer (*Cervus nippon*) hardly displayed bowing behaviour when being fed by humans in comparison to older individuals, but quickly adopted this behaviour through observation (Akita et al. 2016). Also animals can be influenced in consuming a flavoured diet previously eaten by its demonstrator after an interaction time, as was demonstrated with rats (Galef and Stein 1985), dogs (Lupfer-Johnson and Ross 2007) and pigs (Figueroa et al. 2020). Horses are affected simply by the presence of a dominant conspecific by avoiding eating near the high-ranking individual (Krueger and Flauger 2008).

1.3 Analysis of the group's hierarchy and social network

In order to identify effects of social status, relationship quality, kinship or other factors, on the occurrence of social learning, those factors need to be investigated first. Two of the most interesting factors in social group life are hierarchical structures and the relationships between individuals. When interacting with each other, animals show a wide range of interactions towards each other in a positive as well as a negative way. Socio-negative behaviour is expressed as agonistic interactions which are associated with fighting, threats, aggression and submissive behaviour (McGlone 1986). Socio-positive or affiliative interactions can be seen as close proximity to individuals, social grooming or body contact between conspecifics (Massen et al. 2010). Collating and analysing this behaviour can be achieved by social network analysis, as "it provides standardized mathematical methods for calculating measures of sociality across levels of social organization, from the population and group levels to the individual level" (Makagon et al. 2012). Frequent affiliative interactions result in a socio-positive relationship between individuals, which can be compared to friendship (Massen et al. 2010), while agonistic interactions result in a socio-negative relationship.

Agonistic interactions can also allow an insight into the social hierarchy, as higher-ranking individuals show more socio-negative behaviour (Knowles et al. 2004). By observing naturally occurring direct and indirect agonistic interactions, a hierarchy can be established, independent on specific contexts such as competition over food (Langbein and Puppe 2004). In animals living in linear or near-linear societies, animal A dominates B, B dominates C and thus A dominates C (Vries 1998). However, in non-linear societies, animal C might dominate animal A, while A dominates B, and B dominates C. In order to get an insight into such dynamic hierarchy structures, different approaches have been described. For example, dominance can be identified using dyadic tests in which two individuals compete against each other, usually over a monopolizable food source, with the winner being dominant over the loser (David 1987). The winner-loser model on a dyadic level is a popular method to investigate simple hierarchical structures, but sociometric aspects like the stability or strength of relationships describe the hierarchy more detailed and take the analysis onto a group level (Langbein and Puppe 2004).

If hierarchical structure and relationships between individuals of a group are identified, different behavioural patterns can be investigated on this basis. Krueger and Flauger (2008) tested pairs of horses (*Equus caballus*) for their feeding strategy when a dominant demonstrator was fed from a bucket while the other horse was observing. The observing horse avoided feeding from the same bucket as the demonstrator, when the demonstrator was tied up next to it (Krueger and Flauger 2008). The absolute rank of the test subject can also influence behaviour towards conspecifics: Dominant long-tailed macaques (*Macaca fascicularis*) showed more prosocial behaviour in granting itself and its neighbour a slice of banana than subordinates who only rewarded themselves with food (Massen et al. 2011). In the context of feeding behaviour, subordinate white-faced capuchins (*Cebus capucinus*) preferred to stay at the rim when foraging in a group. The authors suggested that the reason could be avoiding high-ranking individuals feeding in the centre (Hall and Fedigan 1997).

Also, frequent affiliative behaviour between individuals influences their behaviour. If animals regularly show affiliative behaviour towards each other (e. g. physical contact, staying in close proximity), Massen and colleagues suggested that the term “friendship” can be applied (Massen et al. 2010). These special bonds occur for example in an East African chimpanzee community where females even form small groups (“cliques”) and the author suggested that these bonds decrease the cost of competing over food resources (Wakefield 2013). In chacma baboons (*Papio ursinus*) social affiliation brings advantages, mainly to the leader, as King and colleagues (2008) demonstrated. Low-ranking individuals followed their leader to a competitive experimental food patch due to their social bond, although not benefiting from the dominant-led decision (King et al. 2008). A study with cattle (*Bos taurus*) hypothesized, that allogrooming correlates with spatial proximity, as cows being frequent neighbours at the feeder showed this behaviour pattern more often (Val-Laillet et al. 2009). The impact of social contact on the behaviour can also be observed in another common farm animal: the pig. When piglets are granted free access to neighbouring pens and can socialize with other piglets besides their siblings from the first day, they show less agonistic behaviour and therefore less severe skin lesions after weaning and regrouping than the control group, where unacquainted pigs were thrown together (Kutzer et al. 2009). But allowing piglets close social contact within a pen is also important for an optimal weight gain, as they showed more food intake when being able to observe and interact with their mother over solid food (Oostindjer et al. 2011).

1.4 Behaviour in pigs (*Sus scrofa*)

These last examples have shown that social contact between pigs has an impact on their behaviour, but also their complex hierarchy makes them an interesting study subject.

Pigs live in a matriarchal herd with two to four sows and their recent litter. The boars range in bachelor groups and join the sows only during the reproductive season (Keeling and Gonyou 2001). They live in a stable hierarchy established after weaning with the most dominant pig on top. The highest-ranking sow asserts herself during competing over food. Next in line is the second pig, in the ranking below the first, but above the third individual, and following this scheme on to the lowest-ranking pig. However, there is a phenomenon called “special relation” where several pigs can occupy the same rank and “triangular” relations, where one pig can dominate the other despite being lower-ranking (Signoret et al. 1975).

Studies have shown that pigs can 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). Another behaviour pattern displayed by pigs with an affiliative relationship is social nosing, which means that they gently touch another pig’s body part with their nose (Camerlink and Turner 2013). Also auditory signals can occur between two individuals, for example a repeated grunt as greeting, followed by the same grunt from its counterpart (Kiley 1972).

The opposite of affiliative behaviour manifests itself as agonistic behaviour like “head to body knocks”, “parallel/ inverse pressing”, “bitings” etc. (Puppe 1998). Especially boars display specific behaviour like raising their bristles on the back, gnashing with their teeth or pawing the ground (Signoret et al. 1975). Also the position of two fighting pigs gives information about the role of the two battlers: offensive attacks often start from the side towards the ears (“T-shape”), whereas defensive pigs can avoid getting bitten towards the face by standing side by side but facing opposite directions (“reverse parallel”) or the same directions but slightly shifted (“asymmetric parallel”) (Rushen and Pajor 1987). Submissive behaviour is often simple avoidance of a conflict and in extreme cases a high pitched squeal (McBride et al. 1964). Additionally, McClone (1985) hypothesized that a pheromone induced submissiveness at the end of a fight (McGlone 1985).

Especially pigs (*Sus scrofa)*, as highly social animals (Keeling and Gonyou 2001), and with one of the largest functional olfactory receptor genome (Nguyen et al. 2012), rely mainly on their sense of smell rather than their visual sense (H. G. Graves 1984). If housed in a semi-natural environment they spend 52 % of the day rooting and can detect a volatile component of black truffles buried 5 cm underground (Studnitz et al. 2007, Talou et al. 1990). Piglets that are only one day old, are able to distinguish their mother's odour from other sow's and show a clear preference for their mother's odour (Horrell and Hodgson 1992, Morrow-Tesch and McGlone 1990). As Jeppesen (1982) has shown with an artificial udder, piglets can differentiate "their" teat from all the other teats through olfactory cues. After changing the position of teats the piglets would find "their" teat again, furthermore these preferred teats were marked by nuzzling behaviour, an early form of territorial behaviour (Jeppesen 1982). This shows that from an early age on, hierarchy is very important for the group structure.

Various experiments have shown that after social interaction with conspecifics, animals tend to eat the same flavoured food as their demonstrators (Galef et al. 1998, Oostindjer et al. 2011, Ratcliffe and Ter Hofstede 2005). Flavour preference can be transmitted from demonstrators to observers, also referred to as "socially-mediated food-preference learning" (Sclafani 1995). Galef and colleagues conducted many studies with Norway rats and proved the existence of social transmission of food preference (Galef et al. 1988, Galef and Stein 1985, Galef and Whiskin 2001), which can be observed in their daily routine when avoiding poisoned bait (Galef and Clark 1971). Pigs showed also similar favouritism for a flavoured diet when they previously interacted with conspecifics which consumed the same food (Figueroa et al. 2020). Moreover, they showed observational learning when they have watched a sibling finding hidden food and followed its example by discovering the food in the same through (Nicol and Pope 1994). The authors raised the question whether the social status and identity of the demonstrator might have influenced the outcome and if the results would have shown more social learning with more experienced demonstrators, such as their mother. In that regard, Veit and colleagues (2017) conducted a more complex experiment including a feeding apparatus (a wooden box containing food, only accessible by sliding a door to the right or left side) and the piglets' mother or aunt as demonstrators. The piglets copied the pushing direction of their demonstrator but not the initial point of action (left or right side of the door) (Veit et al. 2017).

Held and colleagues (2002) also concentrated on the fact, that pigs follow their knowledgeable conspecifics to food sources and have combined the hierarchical status in their experimental design: Subordinate pigs were informed of the location of a food source and subsequently a naive high-ranking individual joined. By altering their behaviour in response to the dominant pig, the subordinates tried to access the food without leading the dominant to the food source. If the dominant was out of sight or moving away, the low-ranking individual moved closer to the food source (Held et al. 2002). Unfortunately, only the high-ranking individuals were chosen to act as naive foragers and subordinate as informed ones, whereas the behaviour of two pigs with a similar rank would have been equally interesting. Moreover, bearing the fact in mind that close social bonds between pigs exist, the different relationship qualities (positive or negative) might also play a role in foraging situations.

1.5 Aim of this study and hypotheses

All these previous examples highlight the complex group structure of pigs and their preferential exploration of the environment using their exceptionally well-developed sense of smell. Therefore, the current study aims to investigate the influence of rank and relationship quality of 20 female Kune Kune pigs on the preference for food linked to a certain conspecific via connected olfactory cues. Additionally, we examine the differences between the pigs' attention towards conspecifics concerning rank and relationship quality.

We hypothesized that pigs prefer information provided by dominants and individuals with a more positive relationship. Various studies have shown that dominants receive more attention and are often preferred as demonstrators in social learning tasks. A positive relationship quality could mean an easier access to the food and previous experienced reciprocal behaviour. Furthermore, we predicted that pigs would pay more attention during demonstration to the dominants or individuals with better relationship quality compared to subordinates or conspecifics with lower relationship quality.

In order to test our hypotheses, we first presented test subjects (observers) with two pigs (demonstrators) differing in rank or relationship quality, one on the observer's left and one on its right side. Demonstrators were consuming food while the observer was watching. This exposure phase was executed in an outdoor area in front of a test hut. After the exposure phase, the observer could enter the test hut and was able to choose between two food bowls, which were positioned left and right from the entrance. To provide additional olfactory assistance in connecting the food bowls with the respective demonstrator pigs outside of the test hut, the demonstrators were sprayed with olfactory cues that were also applied on cloth strips on the according side in the hut, just above the food bowls. This simulated an exposure of food preference, and enabled the pigs to use their sense of smell in order to make their choice.

For selecting the demonstrators, the hierarchy and social relationship quality had to be assessed. To get an insight into the group’s hierarchy, competition tests were performed, where the pigs had to prevail against a partner by claiming a monopolizable food source. This has proven to be an useful approach to determine a hierarchy (Brouns and Edwards 1994). The social relationship quality was measured by analysing behavioural recordings for socio-positive, socio-negative, neighbouring and mating-related interactions.

2 Methods

2.1 Test subjects

Out of a mixed-sex group of 39 adult Kune Kune pigs (*Sus scrofa domesticus*), only the 20 sows were tested (Tab. 1), as in natural conditions pig sounders mostly consist of sows and their offspring of under 1 year and especially for those individuals effects of relationship quality on social cue use can be expected. The pigs live in semi-natural conditions at the Haidlhof Research Station (Bad Vöslau, Austria). In 2014, three already pregnant sows arrived at the Haidlhof, giving birth to 18 piglets the same year. Another litter was conceived by a breeding boar brought to the research station, resulting in 20 piglets being born one year later. The boars have been vasectomised at the age of four months to prevent not only inbreeding but also to ensure natural behaviour. They have 8 ha of pasture at their disposal, providing *ad libitum* access to fresh grass and herbs. They are additionally being fed with boiled corn and leftover vegetables. The pigs can find shelter in six insulated wooden huts, located in a 1 ha forest. A wallow provides water and mud for cooling and skin care.

Table 1: Names and abbreviations of the pigs: Pigs in bold names are the mothers (born 2013), grey coloured names are deceased. The pigs with cursive written names were born 2014, the rest (underlined) pigs were born in 2015. Females are shaded red.

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

2.2 Ethical statement

As exclusively non-invasive tests, the following behavioural experiments do not qualify as animal experiments under TVG2012. The study is discussed and approved by the institutional ethics and animal welfare committee in accordance with good scientific practice (GSP) guidelines and national legislation (reference number ETK-168/11/2020). All pigs are trained to respond to their individual names when called and will follow the experimenters voluntarily to the various testing compartments. They will always be rewarded for following the experimenter's requests (positive reinforcement only*).* As all individuals of this group live together since their birth, a stable hierarchy was developed, which prevents fights from occurring. However, the proposed hierarchy tests are overseen by at least two experimenters, and should fights arise, the pigs will be separated and let back to the pasture. The selected flavours will not harm the pig´s health in any way and should be instead possibly enriching.

2.3 Rank assessment

2.3.1 <u>Data collection</u>

Competition over a monopolizable food source has proven to be a reliable way to assess the hierarchy within a group of pigs (Brouns and Edwards 1994). In order to assign each Kune Kune pig its rank in the group hierarchy, dyadic hierarchy tests were performed. By a total combination of 741 possibilities to pair two different individuals (N = 39), 244 pairs were tested. Each pig was tested with a minimum of 6 other individuals while the remaining pairs were not tested, as their relative rank could be inferred by the results of the executed tests. Each pair was tested in a minimum of three consecutive test rounds. During the preparation of each test round, a monopolizable food source (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 round, they were let out simultaneously to compete over the food (Fig. 1). The pig that was able to successfully defend the food source was rewarded with one point, the loser with zero points. Afterwards, they were let back in their compartment. In the second test round, the "loser" had a head-start, giving him the possibility to reach the food source before his opponent. This procedure was repeated until one pig had won three times.

Figure 1: Hierarchy test setup. A monopolizable food source was placed in the 8m x 8m arena, then both pigs were let out simultaneously (test round 1).

2.3.2 Data preparation

The whole process was recorded by an overtop network camera, while results were simultaneously noted by the experimenters. The winner of each dyad was scored with one point in the data sheet. However, if neither of the two pigs could prevail over the other, both received 0.5 points. The scores per dyad were entered into a pivot table which was then used to calculate the David's score (David 1987) as a measure of dominance rank. David's scores (DS) were calculated using the R-function "getNormDS" (R-package: "steepness") in R (Version 3.6.1, © 2019 The R Foundation for Statistical Computing).

2.4 Relationship quality assessment

2.4.1 Data collection

From August 2020 to mid-September 2020 the behaviour of all 39 pigs was recorded by hand-held cameras and two stationed network cameras. Every day from 8:00 am to 4:00 pm, three "scans" were performed whereby the entire herd was filmed in its surroundings, its nearest neighbour and its group affiliation. A person walking through the enclosure captured as much behavioural displays as possible while also commenting the recording behaviour. Because technical problems such as bad lightning, insufficient resolution of actions far away or blurred recordings could lead to losing information, the behaviour was commented verbally. Additionally, "*ad libitum*" recordings captured any spontaneously displayed behaviour while walking through the enclosure. Furthermore, the group feedings were recorded every four days, by two stationary cameras positioned atop the two feeding grounds located in the wooden area of the enclosure (Fig. 2).

Figure 2: Feeding video of the two feeding grounds.

A total of 811 scan and *ad libitum* videos were recorded (75 % by two interns), and coded using the behavioural coding program Solomon Coder (beta Version 19.08.02, © András Péter, https://solomon.andraspeter.com). The pig, which was directing behaviour at another pig was coded as active pig, the recipient as passive. Observed behaviour was classified into affiliative, agonistic and mating-related interactions (Tab. 2), as well as group affiliation based on proximity (see Tab. 3).

Affiliative behaviour included greeting, snuffling, touching, co-feeding, co-resting, co-foraging and go after (definitions in Tab. 2). Agonistic behaviour was described as displacement with and without body contact, aggressive displacement, threatening, gnashing of teeth, fighting, chasing alone, chasing in group and defensive vocalisation. Mating related behaviour occurred (mainly) between males and females expressed as sniffing, following, scenting, scent marking, scenting while another male is copulating, prodding, testing, mounting, copulating and flirting. Even though mating-related behaviour mainly occurs between different sexes, specific interactions (e.g. sniffing) were included in the analysis as they have been observed between females, too. Grouping behaviour was coded in terms of proximity. The pigs were assigned to belong to groups when resting not more than a body length apart from each other or when foraging in near distance to each other (within three body lengths). Solitary pigs were coded as a group by themselves with no other members. After a minimum of 15 minutes between video recordings, the group compositions could be newly acquired, depending on the number of *ad libitum* video recordings. During *ad libitum* recordings only the spontaneously occurring interactions were coded (as well as the pigs within the group containing the active and passive pigs), whereas the daily scan recordings followed a fixed schedule (morning, midday, afternoon). In each of the three scans, every pig was recorded at least once. Next to the pigs' interactions, the current weather and the location of the respective pigs (forest, meadows or huts) was specified. During feedings, other spatial specifications regarding the position of the active pig in respect to the rest of the group (rim, centre, outside) were also coded. Due to the separate positions of the feeding grounds, the pigs were assigned to the feeding group according to their primary appearance on one of the two feeding grounds. Because the feeding took approximately twenty minutes and a huge amount and variety of behaviour was displayed, each time only the first five minutes were coded. Furthermore, repetitive interactions within one interaction bout between two pigs were only analysed once as it could misrepresent more active individuals. In case a pig would stay out of the range of the camera during the whole 5 minutes of the coded feeding video, making it not assignable to one of the two groups, it was encoded as solitary pig somewhere in the forest.

Table 2: Affiliative, agonistic and mating-related behaviour and its definitions

Behaviour	Abbreviation	Definition
Affiliative		
Greeting	Gr	pig A vocalises towards pig B's head
Snuffling	Su	pig A touches nose of pig B
Touching	To	pig A touches head or other body parts of pig B
Co-feeding	Cf	pig A eats next to, or slightly behind, pig B at the feeding ground, within a radius of a pig's head
Co-foraging	Co	pig A grazes next to pig B at the meadow, not more than three body lengths apart, pig A is slightly behind pig B
Co-resting	Cr	pig A lies next to pig B with body contact
Go after	Ga	pig A follows in path of pig B in a maximum distance of three body lengths
Agonistic		
Displacement without body contact	Di	pig A walks in direction of pig B, not necessarily aggressive, pig B leaves or makes a detour, no body contact
Aggressive displacement	Ad	(fast) aggressive approach of pig A towards pig B, pig B runs off, without body contact
Displacement with body contact	Dw	pig A displaces pig B with pushing, biting; pig B runs off
Threatening	Th	pig bends back, raises hair and ears to impress competitor, or two pigs walk/stand shoulder to shoulder
Gnashing of teeth	Gn	pig A grinds teeth and starts foaming, pig B = NN
Fighting	Fi	pig A and pig B are pushing, biting, scratching each other and sometimes there is also a vocalisation
Chasing alone	Ca	pig A runs after pig B
Defensive vocalization	De	pig A screams (vocalizes loud/sometimes quietly) into side of face of pig B, often alert ear position, L-shaped position of pigs
Mating-related		
Sniffing	Si	pig A sniffs at another's bottom
Following	Fw	male is running or going after the female, often with body contact and vocalizations
Scenting	Sc	pigs sniff at each other's snout; the male is foaming; without vocalization
Scent marking	Sm	pig is setting a mark by rubbing the forelegs on the ground
Prodding	Pr	males prod or push the female's head and/or abdomen
Testing	Te	pig A puts head on back of pig B, trying to mount, pig B goes away
Mounting	Mo	pig A climbs on pig B's back; pig B is standing still; without copulation
Copulating	Cp	male mounts female and inserts penis into the sow's vagina
Flirting	Fl	male "greets" female, after other mating related behaviours were

		shown

Table 3: Grouping behaviour and its definitions

Behaviour	Abbreviation	Definition
Grouping		
During foraging	df	pigs are in the same distance to each other and / or moving in the same direction, standing as well as foraging
During feeding	fe	pigs associated by the same feeding place location
During resting	dr	pigs lying next to each other, within one body length apart
Nearest neighbour	NN	pig B is closest to pig A

2.4.2 Data preparation

In order to calculate the relationship quality (RQ) of each individual with all the other individuals of this group, we first calculated the sum of affiliative, agonistic and mating related behaviours respectively, for each dyad. Each individual of each dyad was assigned with its own sums, as interactions were recorded in a directed manner (active/passive). This allowed a nuanced relationship quality assessment as the behaviour of each individual was considered, instead of merging interactions of both individuals of a dyad.

All sums were then adjusted for the number of actual observations of the respective individual to control for different observation times between individuals. The adjusted sums were then standardized by converting them into z-values, to make the different behaviour categories (affiliative, agonistic and mating-related) comparable. The z-values of the adjusted sums were then added together with affiliative and mating-related behaviours as positive values and agonistic behaviours as negative values. This resulted in relationship quality scores for each individual. If the RQ scores were positive, the individual displayed more affiliative (and mating-related) behaviours towards the respective partner, than agonistic behaviours. In contrast, if those RQ scores were negative, the individual generally had a higher output of agonistic compared to affiliative behaviour towards the respective partner. However, negative RQ scores could also be assigned when no positive and no negative interactions were observed (for an example see Tab. 5, dyad B0-B11). This was due to the fact that the z-value displays the mean sums of the behaviours as zero, and no positive interactions are therefore calculated as below average (negative value).

2.5 Test procedure

In order to test for the effects of the established rank and relationship quality between individuals, 20 female observers were tested in four test rounds in which they were first presented with two demonstrators differing either in their rank or relationship quality to the observer (exposure phase), after which they were allowed to choose between two food bowls spatially and olfactory connected to the respective demonstrator (test phase). Each observer was tested in one test round per week over four weeks. In total, 80 tests were conducted.

2.5.1 Testing environment

The tests took place in a 6 m x 6 m test hut with three adjacent outdoor compartments (2 m x 2 m) and a waiting area (6 m x 2 m), each separated by a metal fence (Fig. 3). The middle compartment of the three outdoor compartments was used as observer compartment, whereas the two outer compartments were designated demonstrator compartments.

In each of the two demonstrator compartments, one food trough was placed in the middle of the fence towards the middle compartment (observer compartment). This resulted in the demonstrators facing the observer, enabling her to see the demonstrators eat and get close enough to perceive olfactory cues applied to the demonstrators.

Visual covers were installed on the outer fence of the outdoor compartments, preventing diversions from the other pigs which generally assembled in front of the gates to the waiting area. The forest floor of the compartments was covered with tarpaulins to enable easier cleaning and to keep the pigs from rooting in the ground.

To let the observer pig enter the test hut in which two food bowls were located on the left and right side of the entrance, the experimenter (E) operated a guillotine door from the inside of the hut. The experimenter was positioned in the middle back of the room, hidden behind a wooden cover. The two food bowls were covered with slim wooden lids and positioned on both sides of the room in equidistance (2.80 m) from the guillotine door (Fig. 4). Two aroma-tainted, wall-mounted cloth strips (set at a height of 50 cm from the ground) provided the additional olfactory cue leading to the two food bowls. The aromas were the same as the ones applied to the respective demonstrators and always matched the side of their position in the outside compartments, therefore providing a guidance besides the respective side.

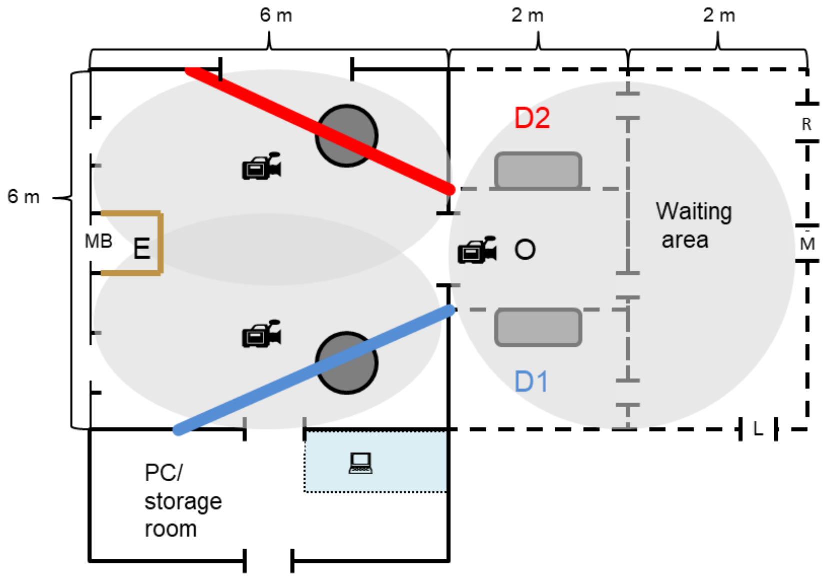


Figure 3: Schematic aerial view of the testing area. The outer section is comprised of the waiting area (accessible for pigs through the right (R) and middle (M) door), the Observer (O), Demonstrator 1 (D1) and Demonstrator 2 (D2) compartments. The experimenter (E) can leave the waiting area also through the left door (L), then entering the test hut through the middle back door (MB) immediately being hidden behind a wooden cover. Inside the test hut are two aroma-tainted cloth strips (blue and red), leading to two food bowls. Two network cameras record the choice inside, one network camera captures the interactions outside. PC and supplies are located in the PC/ storage room.

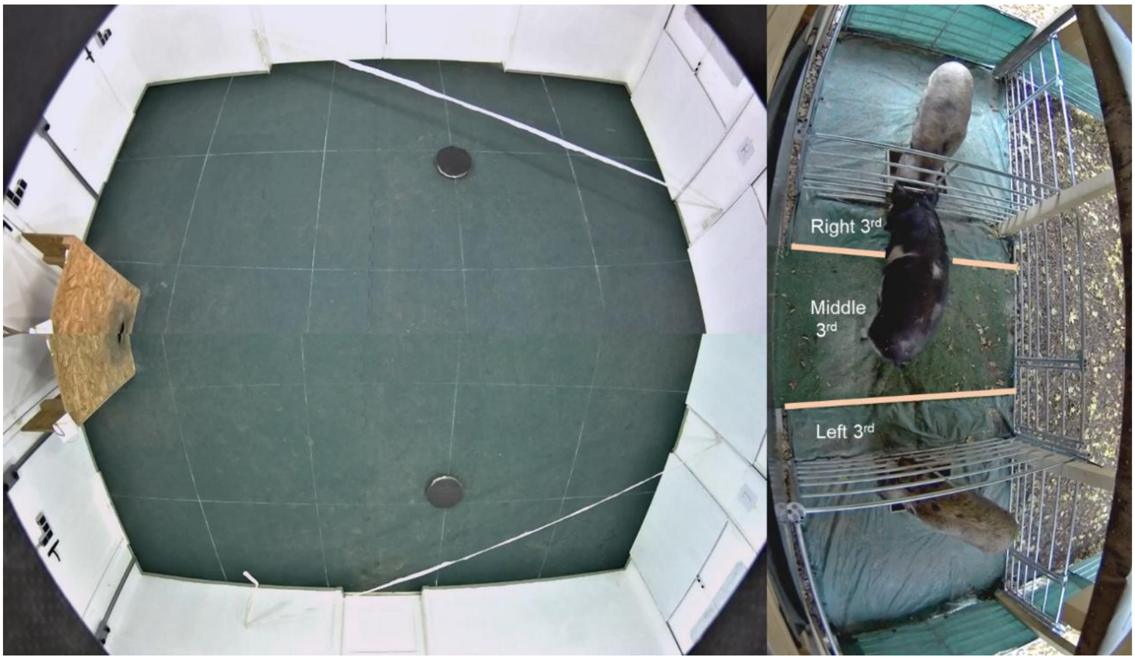


Figure 4: Image from the three network cameras of the hut and the demonstrator and observer compartments. Borders for encoding the observer's position are depicted with the right, middle and left third of the observer compartment.

2.5.2 Olfactory cues

Each pig was assigned with a special aroma (extracts for baking, ordered at ellisaromen.de; see Tab. 4). Each pairing of aroma was previously tested in kinds of olfactory alikeness. This means that the experimenter avoided similar odours, for example two sweet or two spicy aromas. Ten drops of every aroma were then diluted in 100 ml tap water, filled up in spray bottles. The cloth strips were first soaked in water after which a few drops of the pure aroma were added every 10 cm. One cloth strip per pig with its individual aroma container was stored in plastic zip lock bags. Before each usage, the sloth strips were re-tainted with the respective aroma to ensure non-degrading aroma intensity and the diluted olfactory cues were sprayed on the demonstrator pigs' forehead

Table 4: List of aromas. Each aroma was assigned to one specific individual

ID	Name	Aroma	ID	Name	Aroma
B0	Beauty	Olive	R6	Radieschen	Coffee
B1	Bella	Curcuma	R8	Raya	Peanut
B3	Bessy	Parsley	R10	Rosine	Mustard
B4	Bibi	Lime	R11	Rubina	Vanilla
B5	Bijou	Sage	Z0	Zora	Coconut
B6	Blume	Poppy	Z2	Zafira	Fennel
B9	Belana	Hibiscus	Z6	Zoe	Rose
B10	Bernadette	Cinnamon	Z7	Zwetschge	Lavender
B11	Blossom	Ginger	Z12	Zirbe	Fir forest
R1	Rapunzel	Clove	Z13	Zita	Jasmine

2.5.3 Habituation

In order to habituate the pigs to the testing environment, all females could explore the hut individually during two weeks in October 2020. If they did not dare to enter the hut, they had the chance to try again until every female has successfully and voluntarily accessed the hut. The whole process was recorded for further analysis in a different study.

Thereupon, every female was fed three consecutive times in the middle of the hut and also in the two demonstrator compartments with soaked wheat bran. Once again, two cameras captured these proceedings.

2.5.4 Exposure phase

The actual testing took place in November 2020. The demonstrator pigs were called by name and led into the demonstrator compartments with the help of sliced apples and carrots. They immediately started to eat neutrally flavoured and scented wheat bran, which was heavily soaked as it took them longer to finish the wheat bran being in a more wet state. This was important in terms of ensuring a healthy condition as the whole testing procedure took one month and the pigs should not gain additional weight. Subsequently the assigned olfactory cues were sprayed on the demonstrators' forehead. Inside the hut, the cloth strips were attached to hooks on the wall and a few drops of the pure aroma were applied. In the next step, the reward for the observer was prepared, whereat two scoops of formed wheat bran was placed into the food bowls inside the hut and covered with the lids.

When the preparations were done, the three cameras were set to record, and the observer was called by name. Before letting her enter, the demonstrators were sprayed on with the aroma dilution once again and the feed troughs were filled up if necessary.

The observer pig was led into the observer compartment and the timer was set for two minutes, giving her time to interact with the two demonstrators (Fig. 5). The experimenter left the waiting area through the middle door (Fig. 3, M) and circuited the hut without being able to be observed by the tested pig to avoid drawing attention to a certain side of the hut, thereby possibly influencing the behaviour of the observer. After entering the hut through the middle back door (Fig. 3, MB) the experimenter hid behind the wooden cover. When the two-minute exposure phase ended, the experimenter opened the trap door and once the pig was inside immediately closed it again. This marked the beginning of the test phase.

Figure 5: Exposure phase: Positioned on the left hand side is demonstrator 1, in the middle the observer and on the right hand side demonstrator 2.

2.5.5 Test phase

The observer entered the hut and as soon as it chose a food bowl, the experimenter emerged from behind the wooden cover and removed the other food bowl. A food bowl was considered chosen if the pig either touched the lid with its snout or if it removed the lid (Fig. 6). After the pig had eaten its reward, it was led outside into its compartment. Then the video recording was stopped, and the observer was led out of the testing area.

Since all subjects acted both as observer and demonstrator, it was necessary to also prevent side bias development during demonstrations. The demonstrators were therefore given the possibility to gain experience in both demonstrator compartments, by switching places after the test and once again being fed with soaked wheat bran. During this time, the test hut was aired for at least 15 minutes, the cloth strips were demounted, and the food bowls and lids were rinsed with tab water. Finally, the demonstrator pigs were led out of the testing area.

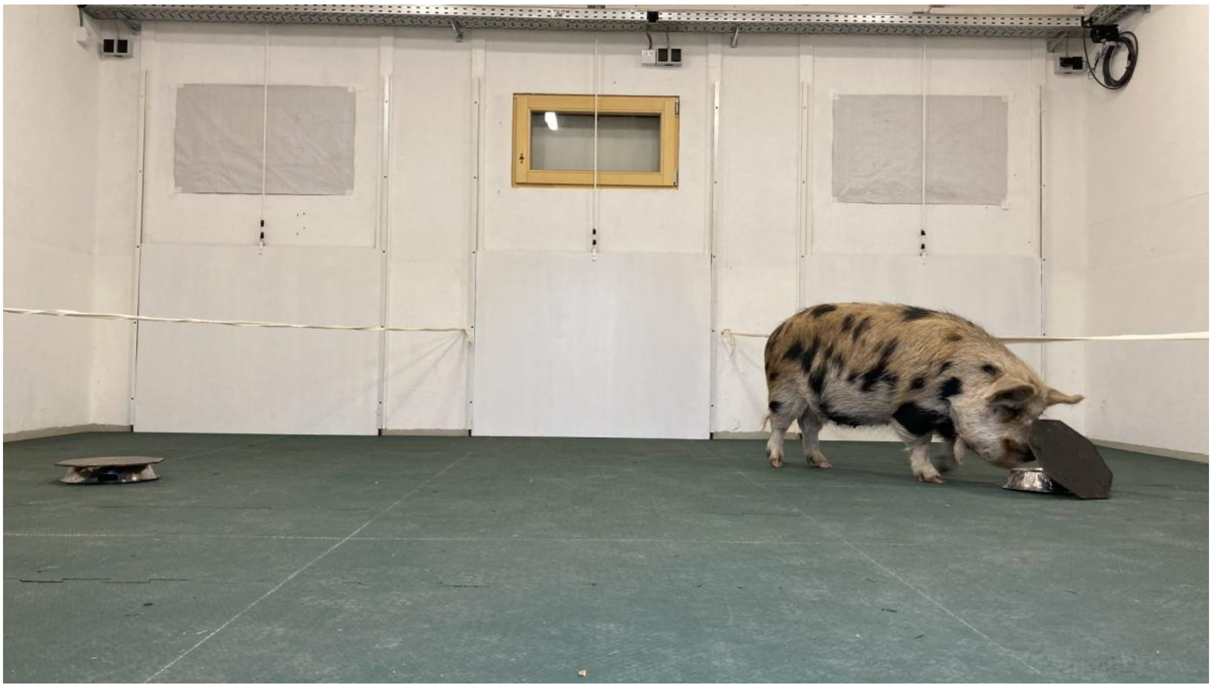


Figure 6: Test phase: The observer chooses the food bowl connected olfactory and spatially with the right demonstrator (Dem 1) by lifting the lid. Shortly after, the experimenter removes the second food bowl (here the left bowl, connected with Dem2) and leads the observer back outside.

2.5.6 Side bias countering procedure

In order to counteract a possibly developing side bias by choosing a bowl in the test hut, every tested pig was once again re-entering the testing hut on each of the respective test days. The pigs had ten possibilities to choose the other side. If an individual managed to do this within 10 trials, the countering procedure was considered successful. This time no demonstrators were present, and no cloth strips were applied. Both food bowls were positioned as in the test, but only the food bowl of the previously rejected side was filled with formed wheat bran. If the pig chose once again the side from the actual test, it was led out into the observer compartment and was given another possibility to choose again. The procedure was repeated until the pig had chosen the filled food bowl, with a maximum of 10 trials. If the pig chose the other previously rejected bowl at the fifth time (trial 5), a value of five was written down. If an individual did not successfully complete the side bias counter, a value of 10 was still written down. These values were analysed for getting an idea, how long it takes them on average to choose the other side. After successfully choosing the other side, the pig had to re-enter the hut two more times while the food was placed in the middle of the hut, to centre the last positive experience. One week later, the next test was executed.

2.5.7 Demonstrator selection

A total of 3,420 possibilities exist to range 20 females in triads consisting of “Observer”, “Demonstrator 1”, and “Demonstrator 2”. In order to test for clear effects of rank and relationship quality, each female was tested with four different demonstrator dyads, resulting in a total of 80 tests. Those demonstrator dyads were selected based on a combination of rank and relationship quality (RQ) differences towards the observer (Tab. 5 and 6). When focusing on the RQ, similarly ranked pigs were chosen as demonstrators, only differing by their relationship quality to the observer (RQ score difference ≥ 1). Likewise, when the rank was in the focus of attention, the pigs had similar relationship quality but varied in their hierarchical position (David’s score difference ≥ 3). Demonstrator dyads were unique for each observer to avoid increased control factors during analysis. This resulted in some compromises regarding perfect matches for certain individuals but dramatically increased the variability of test triads, as not only key individuals were tested, but all subjects were involved, thereby balancing the number of times pigs participated as demonstrators.

To further reduce the number of factors during analysis, each pig was assigned its own specific aroma (Tab. 4).

Table 5: Test categories: Demonstrator pairings based on differences in relationship quality or rank. Positive and negative relationships between observer and demonstrator are abbreviated as + (plus) and – (minus). High-ranking is abbreviated as “hr” and low-ranking as “lr”. Bold are the qualities in focus for each test.

Relationship Quality		***Rank***	
Dem1	*Dem2*	*Dem1*	*Dem2*
hr **+**	hr **-**	**hr** +	**hr** +
lr **+**	lr **-**	**hr** -	**lr** -

Table 6: Example of test category selection: based on dyads with Beauty (B0) as active individual (act) and all remaining females as passive individuals (pas). Per dyad, all positive and mating related (pm.sum) and negative interactions (neg.sum) were summed up. After transforming these parameters in a z-score, the relationship quality score (RQ score) per dyad was calculated. The rank of the passive individual (Rank pas) indicated by the David’s score (DS) was used to identify in which of the four test categories (Test cat) the dyad could fit.

Dyad	act	pas	pm.sum	neg.sum	RQ score	Rank pas (DS)	Test.cat
B0-Z6	B0	Z6	21	16	**-4.499**	12.25	hr+ hr-
B0-B4	B0	B4	16	0	**0.574**	10.50	hr+ hr-
B0-B3	B0	B3	14	2	**0.228**	9.75	lr+ lr-
B0-R11	B0	R11	4	2	**-0.925**	7.75	lr+ lr-
B0-B5	B0	B5	27	2	1.382	**8.75**	hr+ lr+
B0-Z0	B0	Z0	70	4	6.110	**14.25**	hr+ lr+
B0-Z7	B0	Z7	6	10	-3.923	**12.75**	hr- lr-
B0-Z13	B0	Z13	4	2	-0.925	**5.25**	hr- lr-
B0-R6	B0	R6	0	2	-1.386	5.25	
B0-R8	B0	R8	6	0	0.113	5.25	
B0-Z12	B0	Z12	2	0	-0.349	6.25	
B0-B11	B0	B11	0	0	-0.579	6.75	
B0-R10	B0	R10	6	0	0.113	7.75	
B0-B9	B0	B9	4	0	-0.349	8.25	
B0-B10	B0	B10	8	2	-0.464	9.75	
B0-B1	B0	B1	10	2	-0.233	10.00	
B0-B6	B0	B6	16	4	-0.579	11.00	
B0-R1	B0	R1	8	4	-1.271	12.00	
B0-Z2	B0	Z2	23	8	-1.271	12.75	

2.5.8 Data collection

While one network camera (AXIS M3065-V) recorded the actions from the outside, two overlapping network cameras (AXIS M3045-WV) captured the pig's choice in the testing hut (see Fig.4). All three videos were combined and recorded using OBS Studio (Version 26.1.1, © https://obsproject.com).

In order 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 its compartment and ended when it left through the trap door. The pig was considered to pay attention to one specific demonstrator once her nose was in the left or right third of the observer compartment (see Fig. 4). If the observer's nose remained in the middle third, it was encoded as a neutral position. Because the experimenter wrote down the pigs' choice inside the hut, it was not necessary to encode the recorded video regarding the bowl choice.

2.5.9 Data analysis

Data was analysed using R (Version 3.6.1, © The R Foundation for Statistical Computing). Generalized linear mixed models were fitted using the glmer function (lme4 package), and linear mixed models were fitted using the lmer function (lme4 package). As p-values are not provided with the lmer function, they were calculated using the Anova function (car package). The linear models were fitted using the lm function (stats package). To plot the results, the function plot_model (sjPlot package) was used. For analysing the data of the side bias counter Microsoft® Office Excel® 2007 (12.0.6787.5000) was used.

Model Preparation

Observer rank and mean RQ (sociability)

Even though the main interest of this study was to investigate the effect of demonstrator rank and relationship quality (RQ) on the behaviour of observers, also certain observer traits might interplay with this effect. For example, depending on the observer rank, different reactions could be more likely. Similarly, the mean RQ of the individuals to all other individuals (which might serve as an indicator for general sociability towards others) could lead to different reactions with regard to demonstrator RQ. Since those two traits are based on the same individual, a possible correlation between those factors must be identified before fitting models. Therefore, a Pearson's product-moment correlation was calculated for observer rank and sociability, using the function cor.test (stats package).

Model Descriptions

Observer's choice

In order to investigate whether rank or relationship quality (RQ) had an impact on the observer's bowl choice over the four tests, a generalized linear mixed model (family: binomial) was fitted, using the observer's *bowl choice* (left or right) as dependent variable, and the differences between demonstrator ranks (dem.rank.diff) and demonstrator RQs (dem.rq.diff) as fixed effects. Both values were calculated by using the left demonstrator's values as default and subtracting the right demonstrator's values from them. Positive values would thereby indicate a greater rank or RQ of the left demonstrator compared to the right, whereas negative values would indicate a greater rank or RQ of the right demonstrator.

To control for the effects of *observer rank* (obs.rank) and *demonstrator dyad's combined rank* relative to the observer's rank (dem.rank.rel.sum), a three-way-interaction was used with the fixed effect *demonstrator rank difference*. The *relative demonstrator dyad's combined rank* (relative to the observer's rank) was calculated by adding together demonstrator rank values that were first subtracted with the observer rank values. This was done to control for the fact that each demonstrator combination had its own rank difference to the observer.

Similarly, the *demonstrator dyad's combined RQ* (dem.rq.sum) was added into another three-way-interaction with the variables *demonstrator RQ difference* and *observer rank*, to control for the effect of demonstrator combination with regard to the RQ to the observer.

The *test number* (test.nr) was included to check if the test order had an overall effect on the choice. As the observation time could have had an influence on the observer's choice, the *relative observation time* (obs.time.rel) was included as a fixed effect. The *relative observation time* value was again based on the observation time of the left demonstrator, subtracting it with the observation time of the right demonstrator, in order to make it comparable to the other fixed effects. *Observer ID* (obs.id) was included as a random effect, to control for the fact that certain individuals might behave completely different than the rest. The demonstrator IDs could not be included as random effects as model complexity was too great which prevented the model to converge. Similarly, random slopes could not be included for this reason.

```
choice.side ~ dem.rank.diff * dem.rank.rel.sum * obs.rank +
              dem.rq.diff * dem.rq.sum * obs.rank +
              test.nr + obs.time.rel + (1 | obs.id)
```

Relative observation time

In order to investigate, whether demonstrator rank or RQ might have also had an effect on the attention of the observers towards the demonstrators, a linear mixed model was fitted using the *relative observation time* (obs.time.rel) as dependent variable. Again, two three-way-interactions were used to test for effects of demonstrator rank and RQ differences, while additionally controlling for the *observer rank* (obs.rank), the *demonstrator dyads' combined rank* (dem.rank.mean), as well as the *demonstrator dyads' combined RQ* (dem.rq.sum). The *test number* (test.nr) was included to check if the test order had an overall effect on the choice. *Observer ID* (obs.id) as well as the *demonstrator IDs* (L.dem.id and R.dem.id) were included as random effects.

```
obs.time.rel ~ dem.rank.diff * dem.rank.mean * obs.rank +
               dem.rq.diff * dem.rq.sum * obs.rank +
               test.nr + (1 | obs.id) + (1 | L.dem.id) + (1 | R.dem.id)
```

Total observation time

In order to test whether the *total amount of time* the observer would pay attention to the demonstrators (obs.time.total) would decrease over the *number of tests* (test.nr) another linear mixed model was fitted. Additionally, the model tested for the effect of the *demonstrators dyads' combined rank* (dem.rank.mean) in combination with the *observer's rank* (obs.rank), as depending on the rank of the observer especially low-ranking, or especially high-ranking demonstrator dyads might be of less interest or too intimidating to look at for longer periods of time. Similarly, the model included the *demonstrator dyads' combined RQ* (dem.rq.sum), also in combination with the *observer's rank* (obs.rank), as the observer might not be interested in for example especially low RQ dyads (that would differ in rank). *Observer ID* (obs.id) as well as the *demonstrator IDs* (L.dem.id and R.dem.id) were included as random effects.

```
obs.time.total ~ dem.rank.mean * obs.rank +
                 dem.rq.sum * obs.rank +
                 test.nr + (1 | obs.id) + (1 | L.dem.id) + (1 | R.dem.id)
```

Demonstrator Left-Right distribution

To validate the counterbalanced left-right distribution of the demonstrators for each test with regard to rank and RQ, respectively, two linear models were fitted in order to test for a deviation from zero of the dependent variables (a) *demonstrator rank difference* (dem.rank.diff) and (b) *demonstrator RQ difference* (dem.rq.diff) for each of the four tests, using the *test number* (test.nr) as a fixed effect.

dem.rank.diff ~ test.nr

dem.rq.diff ~ test.nr

Side Bias Counter

In order to describe the side bias results, an average number of trials to success (until the bowl was chosen, that was the opposite of the one chosen in the previous two-choice test) was calculated for each test using the function (=MITTELWERT). The standard error was calculated using the function (=STABW).

3 Results

3.1 Rank and relationship quality assessment

The highest-ranking female with a David's score (DS) of 14.25 is Zora, followed closely by Beauty (DS = 13.75). On the bottom of the hierarchy are Radieschen, Raya and Zita, each with DS = 5.25 (Tab. 7). The median is represented by Bessy and Bernadette with a value of DS = 9.75. All pigs with a DS equal or above the median are considered to be high-ranking (N = 11), whereas pigs with a DS below the median are considered low-ranking (N = 9).

When looking at the mean RQ score per individual (also referred to as sociability score, SS) a z-value above zero means the animal has a higher-than-average sociability, whereas below zero means the animal has a lower-than-average sociability (Tab. 7). The highest sociability score of the group had Bessy (SS = 0.78), while Zwetschge had the lowest value (SS = -2.173). The median sociability score is 0.24, lying between Rapunzel (SS = 0.21) and Bibi and Bijou (both SS = 0.27). The pigs above the median SS are considered to be social (N = 10), whereas the pigs below the median SS are considered less social (N = 10).

Table 7: Rank and sociability per individual pig. Individuals considered to be dominant are shaded red (DS ≥ 9.75). Individuals considered to be less social are shaded blue (SS < 0.24).

ID	Name	Rank (DS)	Sociability (SS)	ID	Name	Rank (DS)	Sociability (SS)
B0	Beauty	13.75	-0.43	R6	Radieschen	5.25	0.026
B1	Bella	10	0.65	R8	Raya	5.25	0.011
B3	Bessy	9.75	0.78	R10	Rosine	7.75	0.312
B4	Bibi	10.5	0.27	R11	Rubina	7.75	0.408
B5	Bijou	8.75	0.27	Z0	Zora	14.25	-0.656
B6	Blume	11	0.14	Z2	Zafira	12.75	-0.595
B9	Belana	8.25	0.44	Z6	Zoe	12.25	-0.865
B10	Bernadette	9.75	0.30	Z7	Zwetschge	12.75	-2.173
B11	Blossom	6.75	0.36	Z12	Zirbe	6.25	-0.187
R1	Rapunzel	12	0.21	Z13	Zita	5.25	0.740

3.1.1 Correlation of rank and mean RQ (sociability)

The Pearson's correlation coefficient ($r = -0.547$, $t = -2.775$, $df = 18$, $p = 0.012$) indicates a strong negative linear correlation between an individual's rank and sociability (Fig. 7). Higher-ranking females had a low sociability score (SS), whereas low-ranking females showed a positive SS. The lowest-ranking females (Radieschen, Raya and Zita: DS = 5.25) have a sociability score of 0.026, 0.011 and 0.740, whereas the three highest-ranking females (Zora: DS = 14.25, Beauty: DS = 13.75, Zwetschge: DS = 12.75) exhibit negative SS of -0.66, -0.43, and even -2.17. Based on this linear correlation, only one of the traits was used as a predictor in the following models. As rank was established via the means of controlled testing, instead of observations (through which an observer bias might occur), the observer rank was chosen as the more reliable factor.

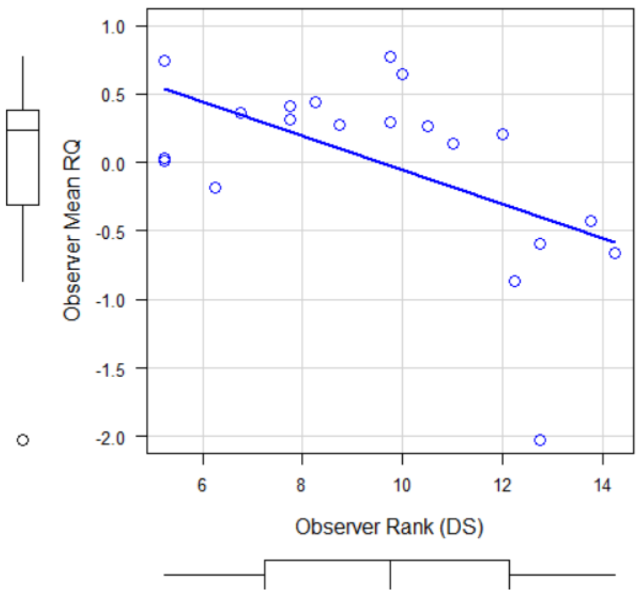


Figure 7: The correlation between Observer Rank and Observer Mean RQ. Dots represent individuals. Box-Whisker plots beside the axes depict data distribution.

3.2 Two choice tests

3.2.1 Observer's choice

To test whether the observer's choice for one of the two bowls inside the hut was impacted by the two-minute exposure phase before entering the hut, a model was fitted using demonstrator RQ and demonstrator rank differences as main predicting factors. Furthermore, effects of observation times during demonstration and the number of tests were included.

Effect of demonstrator RQ

The demonstrator RQ has a significant effect on the observers' bowl choice during the test. In general, the lower the relative RQ of the demonstrator, the more likely the observer would choose the associated bowl (x = -1.478, se = 0.723, z = -2.045, p = 0.041; Tab. 8). However, when combined with the rank of the observer itself, the result becomes more nuanced. We found that HR observers were more likely to choose demonstrators with higher RQ than LR observers (x = 0.156, se = 0.068, z = 2.289, p = 0.022; Tab. 8). This result is illustrated in Figure 8, in which the effect of the demonstrators' RQ on the choice is shown for two types of observer ranks. An exemplary low observer rank (DS_{LR} = 6) is depicted in red while an exemplary high observer rank (DS_{HR} = 13) is depicted in blue.

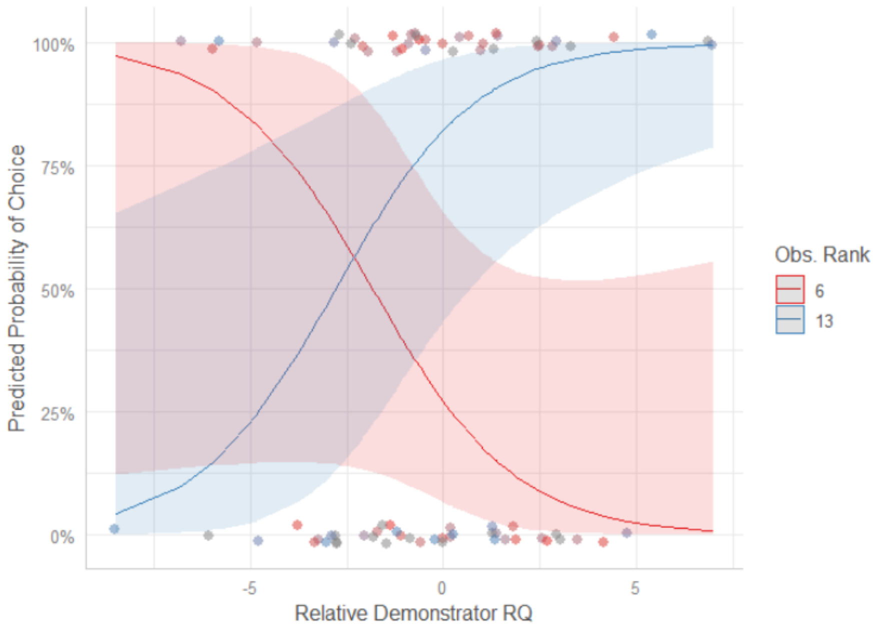


Figure 8: Predicted probability of choice depending on relative demonstrator RQ, exemplary for two observer ranks. Low-ranking observers are coloured red, high-ranking observers are blue. Dots represent individual observer's choice. Predicted probabilities (lines) are plotted with a 95 % CI**.**

Effect of demonstrator rank

The demonstrator rank has also a significant effect on the bowl choice. High-ranking observers (DS = 13) were more likely to choose the relatively lowest-ranking demonstrator, when both demonstrators were ranked lower than the observer. In contrast to that, low-ranking observers (DS = 6) preferred the lowest-ranking demonstrator when both demonstrators were ranked higher than the observer (x = 0.012, se = 0.006, z = 2.046, p = 0.041; Tab. 8). The results are depicted in Figure 9 for low-ranking (left) and high-ranking (right) observers. Exemplary values for the combined rank of the demonstrators are depicted in red and blue, whereby red stands for two lower-ranking demonstrators in comparison to the observer and blue for two higher-ranking demonstrators in comparison to the observer.

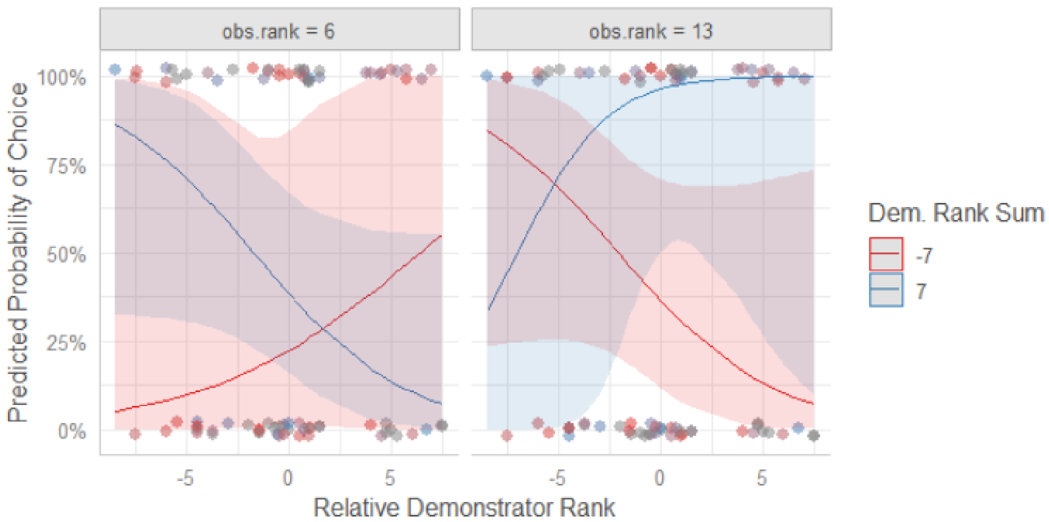


Figure 8: The predicted probability of choice for low-ranking (left) and high-ranking (right) observers based on the relative demonstrator rank. The different demonstrator rank categories (Dem. Rank Sum) were represented exemplary for lower-ranking demonstrators with a demonstrator rank sum of -7 (red) and higher-ranking demonstrators with a demonstrator rank sum of +7 (blue). Dots represent the individual’s choice. Predicted probabilities (lines) are plotted with a 95 % CI.

Effect of relative observation time

A factor which significantly influenced the observer's choice was the relative observation time. The more time an observer spent watching a specific side, the less likely they would choose that side (x = -0.037, se = 0.017, z = -2.202, p = 0.028; Tab. 8).

Figure 10 illustrates the predicted probability of choice when taking the relative observation time in consideration. Observers were more likely to choose the demonstrator's side, when they spent relatively less time watching it.

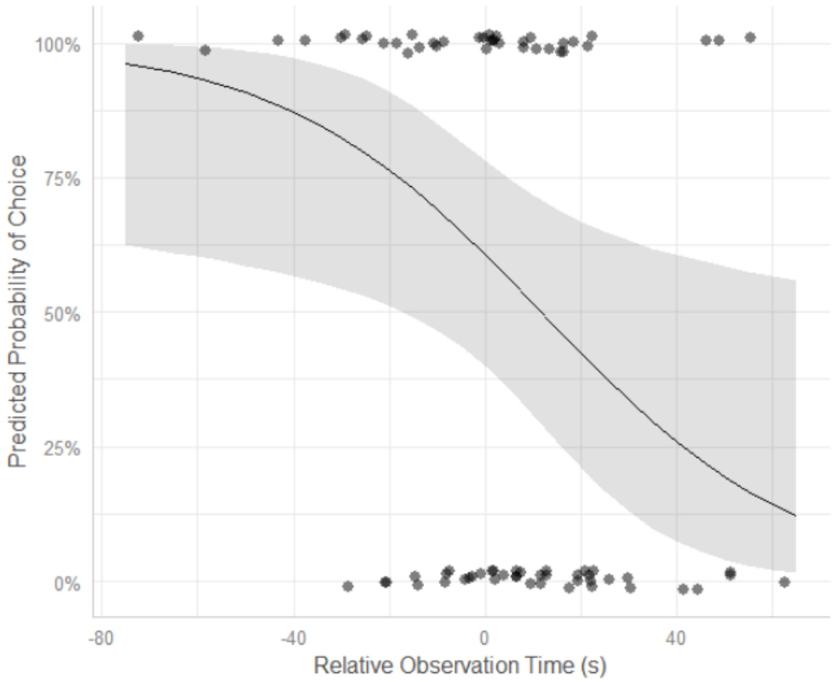


Figure 90: Predicted probability of choice dependent on the relative observation time. Dots represent individual observer's choice. Predicted probability (line) is plotted with a 95 % CI.

Effect of test number

Another significant factor influencing the observer's choice was the test number. When evaluating if the test number influenced the observer's choice, a clear decreased number of left choices over the course of the four tests can be observed (x = -0.688, se = 0.310, z = -2.221, p = 0.026; Tab. 8). The more tests were done, the less likely the observers would choose the left side (Fig. 11).

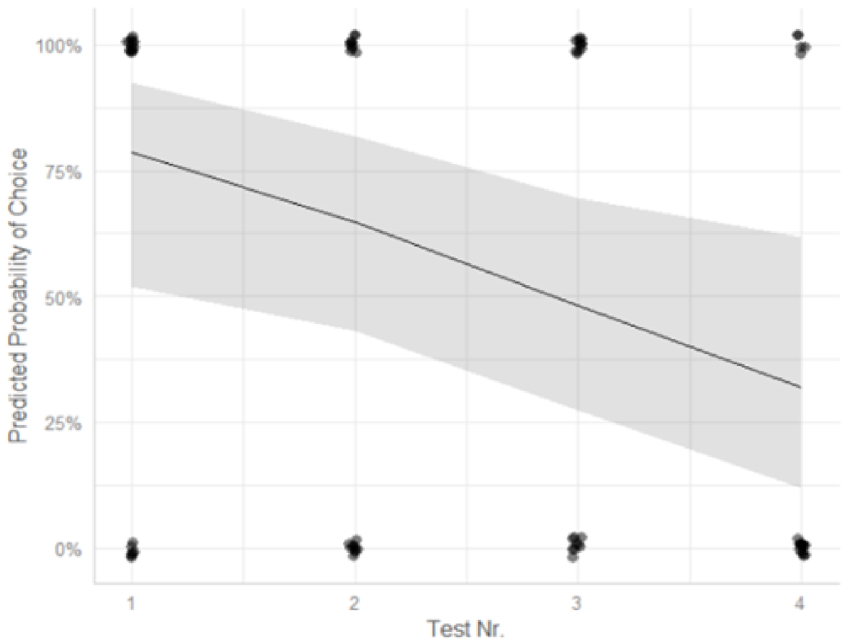


Figure 11: Predicted probability of choice during each test number. Dots represent individual observer's choice. Predicted probability (line) is plotted with a 95 % CI.

Table 8: Calculated values of the GLM for choice. Bold values are significant.
Significant codes: 0 ‘***’, 0.001 ‘**’, 0.01 ‘*’, 0.05 ‘.’, 0.1 ‘ ‘ , 1

	Estimate	Std.Error	z-value	Pr(>|z|)	Sign.
(Intercept)	-1.258	2.266	-0.555	0.579	
dem.rank.diff	-0.159	0.639	-0.249	0.804	
dem.rank.rel.sum	-0.132	0.218	-0.605	0.545	
obs.rank	0.357	0.220	1.622	0.105	
dem.rq.diff	**-1.478**	**0.723**	**-2.045**	**0.041**	*
dem.rq.sum	0.798	0.767	1.039	0.299	
test.nr	**-0.688**	**0.310**	**-2.221**	**0.026**	*
obs.time.rel	**-0.037**	**0.017**	**-2.202**	**0.028**	*
dem.rank.diff:dem.rank.rel.sum	-0.106	0.062	-1.715	0.086	
dem.rank.diff:obs.rank	0.020	0.067	0.295	0.768	
dem.rank.rel.sum:obs.rank	0.031	0.023	1.370	0.171	
dem.rq.diff:dem.rq.sum	0.281	0.338	0.833	0.405	
obs.rank:dem.rq.diff	**0.156**	**0.068**	**2.289**	**0.022**	*
obs.rank:dem.rq.sum	-0.070	0.069	-1.008	0.314	
dem.rank.diff:dem.rank.rel.sum:obs.rank	**0.012**	**0.006**	**2.046**	**0.041**	*
obs.rank:dem.rq.diff:dem.rq.sum	-0.026	-0.026	-1.001	0.317	

3.2.2 Relative observation time

When checking which demonstrator qualities had the most impact on the observers' relative observation time, a model was fitted with the rank and RQ difference as main factors of influence. Moreover, the test number was included as random effect.

Effect of demonstrator rank

The relative rank of the demonstrator had an impact on the relative observation time. If one demonstrator had a higher rank than the other (Fig. 12), the observer would spend more time on the relatively lower-ranking demonstrator side (x = -49.711, se = 15.570, t = -3.193, χ^2 = 3.995, df = 1, p = 0.046; Tab. 9).

When including the factor of demonstrators' combined rank, the results show that there is no difference between dominant or subordinate observers (x = -0.599, se = 0.161, t = -3.732, χ^2 = 13.930, df = 1, p < 0.001). As Figure 13 illustrates, low-ranking observers (DS = 6) spend more time near the lowest-ranking demonstrator, if both demonstrators are ranked low. Likewise, high-ranking observers (DS = 13) also prefer the lowest-ranking demonstrator of two high-ranking demonstrator combination.

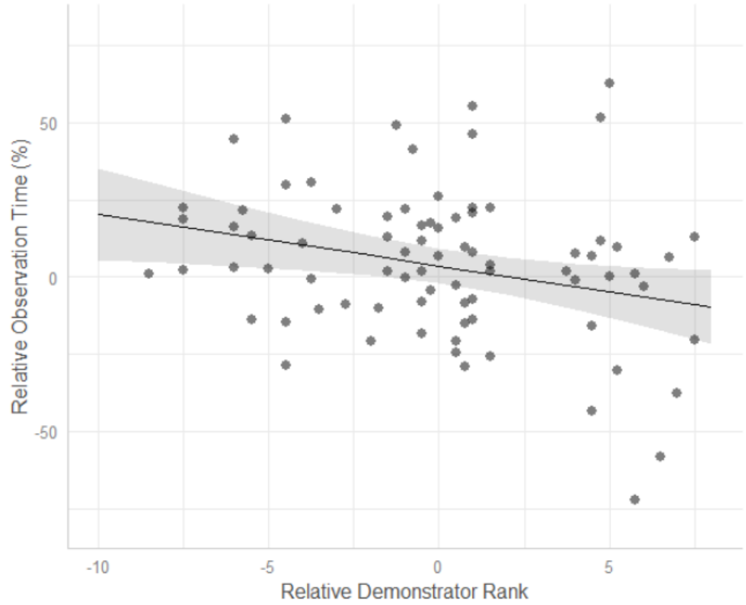


Figure 10: Relative observation time (%) depending on the relative demonstrator rank. Dots represent individual observer's choice. Predicted probability (line) is plotted with a 95 % CI.

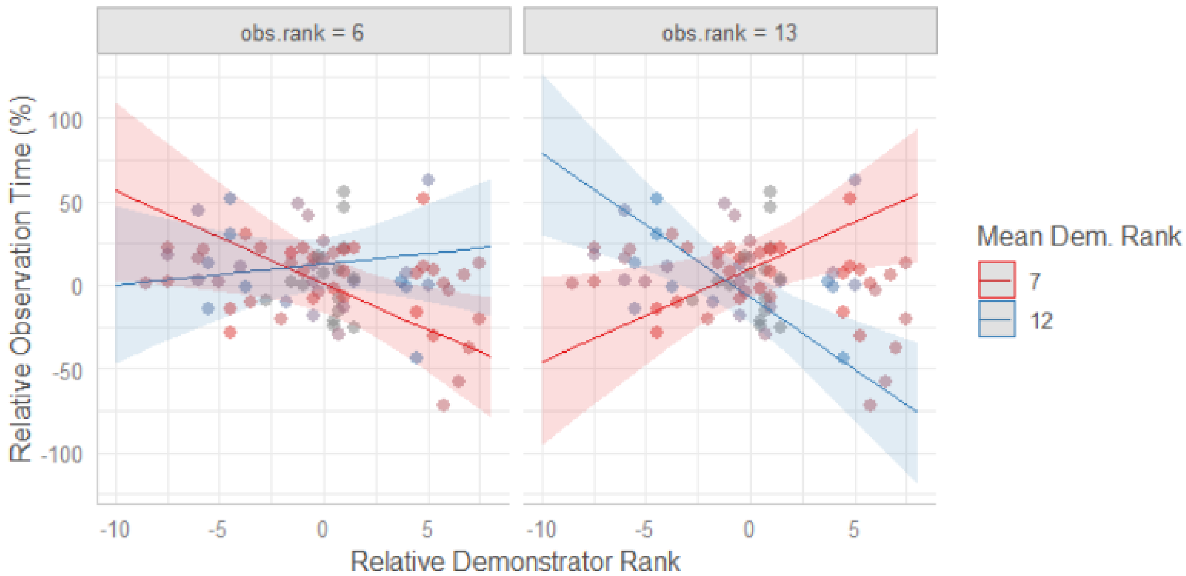


Figure 11: Relative observation time (%) depending on the relative demonstrator rank for a low (red) and high (blue) mean demonstrator rank. On the left side the results for low-ranking observers are illustrated, on the right side are the results for high-ranking observers. Dots represent individual observer's choice. Predicted probabilities (lines) are plotted with a 95 % CI.

Effect of demonstrator RQ

The chi-squared test revealed a significant effect of demonstrator RQ on the observation time of the observer. However, this result is to be taken with caution, as the SE is very high in comparison to the model estimate, resulting in a low t value (x = 0.962, se = 2.135, t = 0.451, χ^2= 4.767, df = 1, p = 0.029; Tab. 9). Figure 14 illustrates that observers paired with demonstrators with overall higher RQ (mean dem RQ = 3) spend more time next to the demonstrator with whom they have a more positive relationship. Opposite tends to be the case for the tests in which observers are paired with demonstrators in which the overall RQ is negative (mean dem RQ = -3). Here they seem to stand close to the demonstrator, with whom they have a more negative RQ. But it should be taken into consideration, that there is a lot more variation, as the light red area depicting the CI in the plot shows.

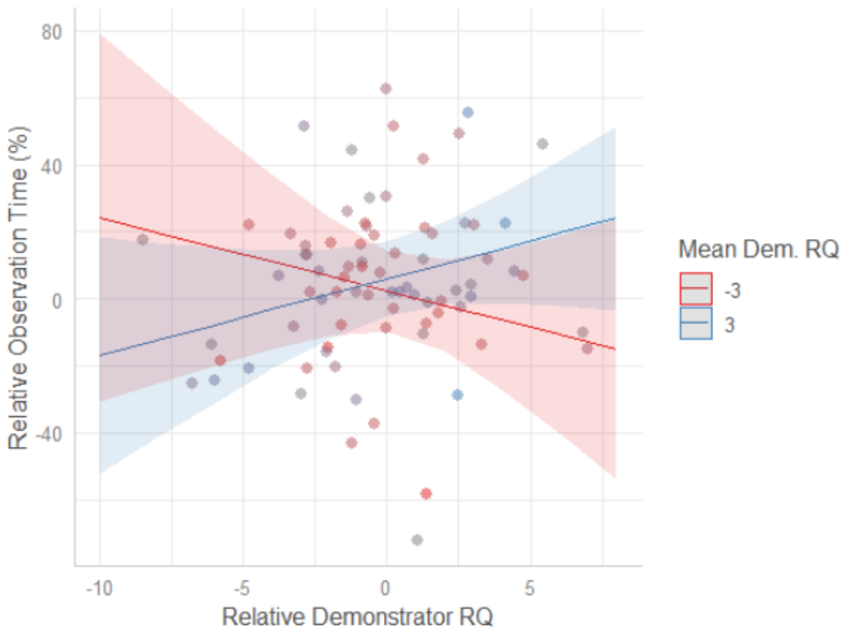


Figure 12: Relative observation time (%) depending on the relative demonstrator RQ for a positive (red) and negative (blue) mean demonstrator RQ. Dots represent individual observer's choice. Predicted probabilities (lines) are plotted with a 95 % CI.

Effect of test number

Even though the test number was shown to have a significant effect on the bowl choice, there was no significant influence on the relative observation time of the observer towards the two demonstrators (x = 0.047, se = 2.325, t = 0.020, χ^2 = 0, df = 1, p = 0.984; Tab. 9).

Table 9: Calculated values of the GLM for the relative observation time. Bold values are significant. Significant codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' ' , 1

	Estimate	SE	t-value	χ^2	DF	Pr(>χ^2)	Sign
(Intercept)	-59.546	56.275	-1.058	-	-	-	-
dem.rank.diff	**-49.711**	**15.570**	**-3.193**	**3.995**	**1**	**0.046**	*
dem.rank.mean	7.390	5.815	1.271	0.013	1	0.909	
obs.rank	7.281	5.765	1.263	0.164	1	0.686	
dem.rq.diff	-5.039	4.273	-1.179	0.113	1	0.737	
dem.rq.sum	0.639	5.360	0.119	0.282	1	0.596	
test.nr	0.047	2.325	0.020	0.000	1	0.984	
dem.rank.diff:dem.rank.mean	4.956	1.624	3.052	1.156	1	0.282	
dem.rank.diff:obs.rank	5.776	1.536	3.760	0.213	1	0.644	
dem.rank.mean:obs.rank	-0.840	0.583	-1.441	2.095	1	0.148	
dem.rq.diff:dem.rq.sum	**0.962**	**2.135**	**0.451**	**4.767**	**1**	**0.029**	*
obs.rank:dem.rq.diff	0.536	0.382	1.403	2.104	1	0.147	
obs.rank:dem.rq.sum	-0.005	0.476	-0.010	0.002	1	0.963	
dem.rank.diff:dem.rank.mean:obs.rank	**-0.599**	**0.161**	**-3.732**	**13.930**	**1**	**0.000**	***
dem.rq.diff:dem.rq.sum:obs.rank	-0.023	0.165	-1.400	0.020	1	0.889	

3.2.3 Total observation time

By checking the factors affecting the total observation time, only the dyad's combined RQ as fixed effect and test number as random effect significantly influenced the GLM.

Effect of demonstrator dyad's combined RQ

The chi-squared test revealed a significant effect of the mean demonstrator RQ on the total observation time (x = -0.168, se = 3.004, t = -0.056, χ^2 = 4.421, df = 1, p = 0.036; Tab. 10). A lower mean demonstrator RQ resulted in more attention of the observers to the demonstrators overall (Fig. 15). Likewise, the higher the mean demonstrator RQ, the less time the observers spent looking towards one of the two demonstrators.
Again, this result has to be taken with caution because the model estimate is very low, while the SE is very high, resulting in a low t value.

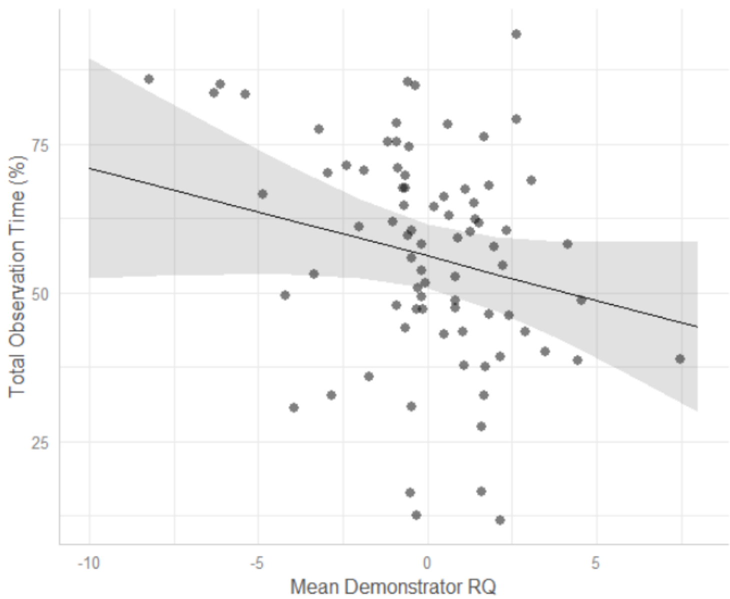


Figure 13: Total observation time (%) depending on the mean demonstrator RQ. Dots represent individual observer's choice. Predicted probability (line) is plotted with a 95 % CI.

Effect of demonstrator dyad's combined rank

The demonstrator dyad's combined rank did not seem to affect the total observation time, neither as a single factor (x = -2.780, se = 3.797, t = -0.732, χ^2 = 1.464, df = 1, p = 0.226; Tab. 10), nor in interaction with the observer's rank (x = -0.139, se = 0.266, t = -0.521, χ^2 = 0.272, df = 1, p = 0.602; Tab. 10).

Effect of test number

The test number had a significant effect on the total observation time (x = -4.219, se = 1.558, t = -2.708, χ^2 = 7.336, df = 1 p = 0.007; Tab. 10). As Figure 16 shows, with increasing test number the total observation time is dropping from 60 % in the first test to 50 % in the last test.

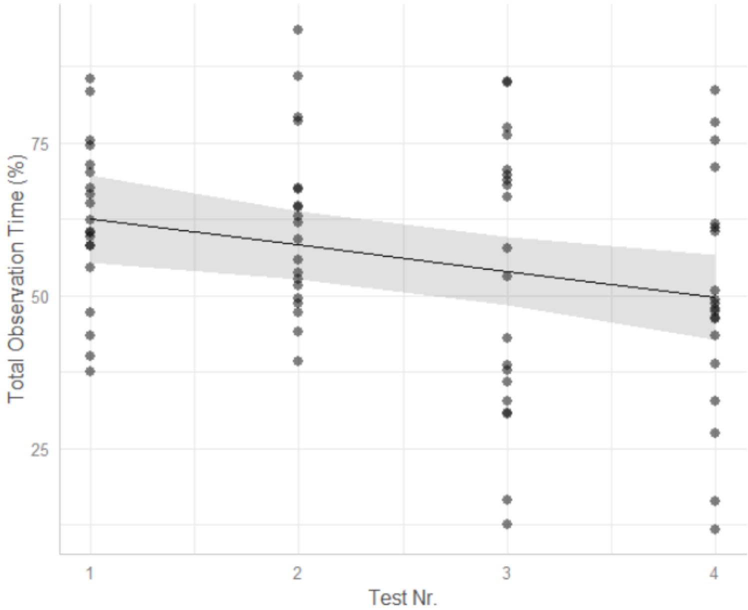


Figure 14: Total observation time (%) over the four tests. Dots represent the individual choice.

Table 10: Calculated values of the GLM for total observation time. Bold values are significant. Significant codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' ' , 1

	Estimate	SE	t-value	χ^2	DF	Pr(>χ^2)	Sign.
(Intercept)	81.337	37.179	2.188	-	-	-	
dem.rank.mean	-2.780	3.797	-0.732	1.464	1	0.226	
obs.rank	-0.346	3.789	-0.091	2.265	1	0.132	
dem.rq.sum	**-0.168**	**3.004**	**-0.056**	**4.421**	**1**	**0.036**	*
test.nr	**-4.219**	**1.558**	**-2.708**	**7.336**	**1**	**0.007**	**
dem.rank.mean:obs.rank	0.168	0.379	0.442	0.196	1	0.658	
dem.rq.sum:obs.rank	-0.139	0.266	-0.521	0.272	1	0.602	

3.3 Demonstrator Left-Right distribution

As Figure 17A shows, the distribution of the demonstrators between left and right was equal considering rank difference (test categories hr+lr+ and hr-lr-) and RQ difference (test categories hr+hr- and lr+lr-), since each test category is present 10 times above and 10 times below the zero mark in its respective axis. Similarly, Figure 17B shows a fairly equal distribution of the different demonstrator combinations over the four tests.

Figures 18A and 18B display the distribution of the demonstrator rank/RQ difference over the four tests in more detail and show little deviation from zero. As evidenced through the fitted linear models, neither the demonstrator rank differences nor the demonstrator RQ differences in the four tests deviated significantly from zero (Tab. 11 and Tab. 12), indicating a balanced test setup.

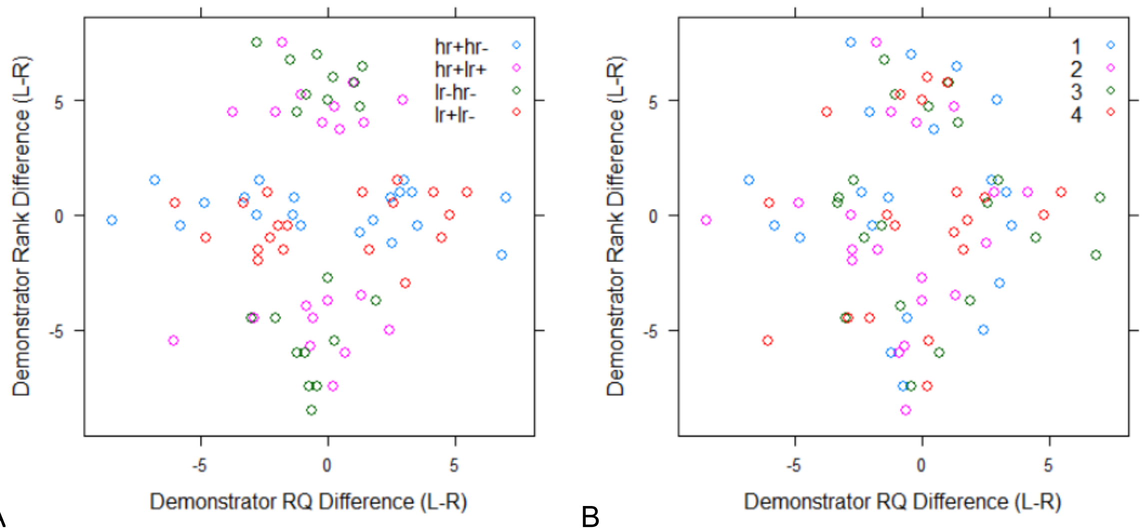
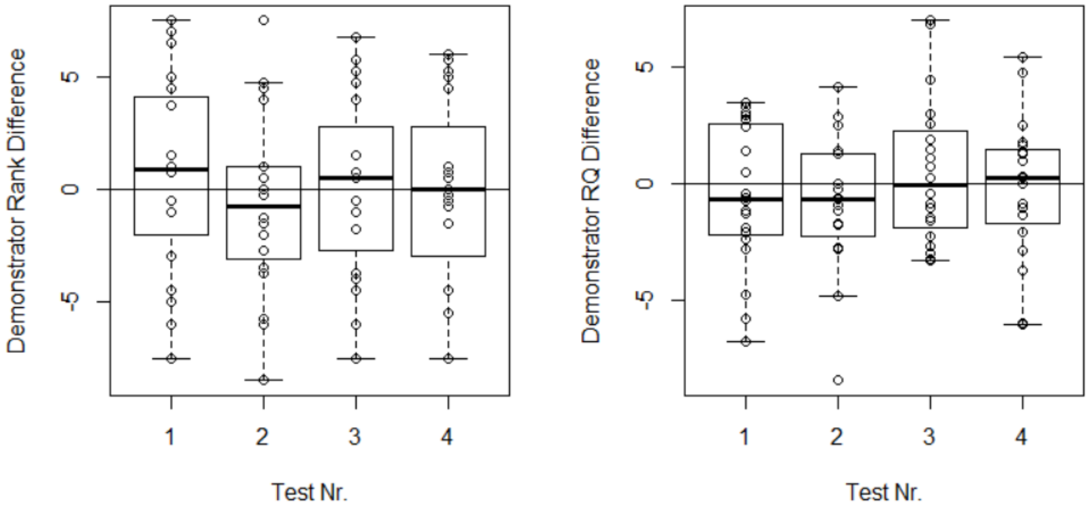


Figure 15: Distribution of demonstrator combinations through the different (A) test categories and (B) test numbers. Demonstrators for the test categories (hr+hr-, hr+lr+, lr-hr- and lr+lr-) were chosen with regard to the difference in rank (hr: high ranking, lr: low ranking) or relationship quality (+: positive, -: negative). Colourful dots represent the respective (A) test categories or (B) test numbers.



A **B**

Figure 16: Boxplots indicating deviation from Zero of (A) demonstrator rank difference and (B) demonstrator RQ difference over the four tests.

Table 11: Deviation from Zero for the demonstrator rank difference. There were no significant differences..

	Estimate.	SE	t value	Pr(>|t|)	Sign
(Intercept)	0.000	0.813	0.000	1.000	
Test Nr. 1	0.575	1.149	0.500	0.618	
Test Nr. 2	-0.625	1.149	-0.544	0.588	
Test Nr. 3	0.100	1.149	0.087	0.931	
Test Nr. 4	-0.038	1.149	-0.033	0.974	

Table 12: Deviation from Zero for the demonstrator RQ difference. There were no significant differences.

	Estimate.	SE	t value	Pr(>|t|)	Sign.
(Intercept)	0.000	0.601	0.000	1.000	
Test Nr. 1	-0.557	0.850	-0.656	0.514	
Test Nr. 2	-0.773	0.850	0.909	0.365	
Test Nr. 3	0.460	0.850	0.541	0.590	
Test Nr. 4	-0.188	0.850	0.221	0.826	

3.4 Side bias counter

As Figure 19 demonstrates, the average trial number throughout the four tests lies between 3 and 4, meaning that the pigs chose in their third to fourth of overall ten trials successfully the other side (Tab. 13). Many pigs (N = 14) succeeded in this test by needing only one trial at times. Only one individual (Zirbe) did not succeed in choosing the other food bowl within 10 trials in Test 4 and was therefore given the maximum trial number. The other test subjects never needed more than eight trials in order to succeed in the side bias counter.

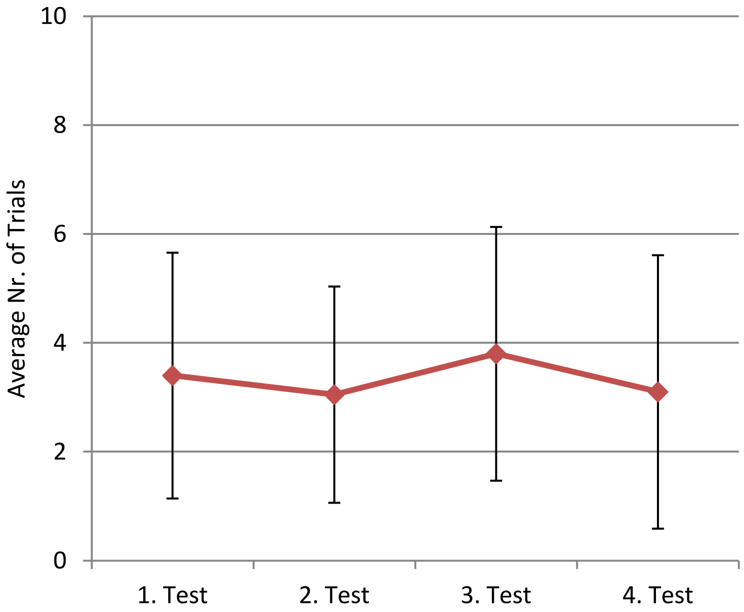


Figure 17: Average number of side bias counter trials over the four tests. Error bars indicate standard error.

Table 13: Average and standard error of the side bias counter trials for all four tests.

	1. Test	2. Test	3. Test	4. Test
Average	3.45	3.05	3.8	3.1
Std. Error	2.212	1.986	2.331	2.511

4 Discussion

The aim of this study was to investigate demonstrator traits such as rank and RQ. Furthermore, their influence on an observer was examined. Therefore, 20 female pigs living in one group were tested with the aid of olfactory cues for accentuating the demonstrators' traits. After completing 80 tests, the results indicate that the observers' rank and RQ have an impact on the choice as well as the observation time. Moreover, the data showed a strong correlation of sociability and rank in female pigs.

4.1 Correlation of sociability and rank

After analysing the data of the rank and RQ assessment, a correlation between rank and sociability could be observed. This is in accordance to other studies, where dominant pigs show more aggressive behaviour than low-ranking individuals, initiate more confrontation and fight for a longer time (Fels et al. 2012, Stukenborg et al. 2011). However, this result may have been in part due to an observer bias, as aggressive behaviour immediately attracts attention when walking through the enclosure while filming. Observers recording the pigs might have unintentionally focused more on the negative behaviour displayed by the more prominent individuals, as the attacked pigs often display defensive reactions like screaming.

4.2 Observer's choice

The GLM for the observer's choice indicated that the relationship quality (RQ), rank, observation time and test number significantly affected the observer pig in its preference for a food bowl.

<u>Effect of RQ</u>

Like predicted, the better the RQ between observer and demonstrator, the more an observer would choose the associated food bowl of the respective demonstrator. However, this result merely applied to high-ranking observers, as low-ranking observers preferred the observer with whom they had a negative RQ.

As for high-ranking observers, tolerated co-feeding behaviour could explain this kind of behaviour. The observer might have preferred the bowl associated with side and olfactory cue of the more affiliative demonstrator with the ulterior motive of being tolerated by the demonstrator and not being shooed away. A study with dogs and wolves has shown that an affiliative relationship guarantees more amicable food sharing among dyads (Dale et al. 2017). In contrast, a master thesis from 2018 with the test subjects of this study found that there was no significant effect of tolerance between affiliative and non-affiliative relationships during co-feeding tests in pigs, only a tendency that amicable dyads showed more socio-positive interactions (Koglmüller 2018).

Furthermore, the results for subordinate individuals should be interpreted with great care due to the relatively broad confidence interval. A possible explanation could be that low-ranking animals are generally less socially competent than high-ranking conspecifics due to their role in the hierarchy. McGuire and colleagues (1994) found a strong connection between social competence and dominance in Vervet monkeys (*Cercopithecus aethiops sabaeus*). Here, higher-ranking monkeys scored higher in the category “social competence” as subordinates (McGuire et al. 1994). Because of their higher rank, they are able to express the full range of interactions, affiliative as well as agonistic. Therefore, in our study, the socially more competent dominants might have chosen the affiliative demonstrator based on their social experience, whereas the result of subordinates choosing the non-affiliative demonstrator could be interpreted as a less reliable by-product.

It should be mentioned that also lower ranking individuals should possess a fair amount of social competence, as they will encounter potentially many aggressive interactions, especially during foraging or feeding situations. In order to avoid those, low ranking pigs should be able to display a higher amount of defensive or avoidance behaviours. Based on this, lower ranking observers might have learned to avoid specific demonstrators, especially the ones with whom they had more previous experiences. This in turn could also point towards an avoidance of demonstrators with better RQ, leading to the aforementioned result. In a review, Galef (1985) wrote that contradictory evidence of avoidance learning can be found in the literature: While rats showed no avoidance of consuming a diet previously consumed by a demonstrator which was poisoned before interacting with the observer, completely different results were discovered with red-wing blackbirds (*Agelaius phoeniceus*), as they displayed a clear aversion (Galef 1985). Nearly 25 years later Masuda and Aou (2009) discovered that a previous bad experience (here an electrical shock when entering a dark compartment) on the observer’s side facilitates avoidance behaviour (thus not entering the dark compartment) when the subject is once again confronted with an experienced partner (which also got an electrical shock) and given the choice to re-enter the compartment. The authors stated that naive individuals were not at all affected by an experienced partner and showed no reluctance to go into the dark compartment (Masuda and Aou 2009).

Although the behaviour of the lower ranking Kune Kune pigs could be interpreted as avoidance behaviour, the circumstances completely differ from the previous studies, which included negative reinforcement. In this study, neither the demonstrator nor the observer pigs were harmed at any time by similar means comparable to poison or electroshock. However, continuous negative interactions with group mates might have contributed to the fact that lower ranking females were less likely to choose the side of the more affiliated demonstrator.

Another explanation for the results of lower ranking females choosing the bowl associated with the demonstrator with the more negative RQ, could be the unintentionally biased recordings of agonistic interactions mainly by high-ranking individuals. Developing this thought further, subordinate individuals in this study may have shown less agonistic behaviour through the 6 weeks in the behavioural recordings, resulting in difficulties for choosing their non-affiliative demonstrators. As described previously, when no clear negative relationship was apparent, individuals with no positive interaction output at all were selected as non-affiliated demonstrators. However, other observers had a non-affiliate demonstrator based on experienced agonistic interactions. Because agonistic interactions are highly associated with the rank, it may have been better to exclude agonistic behaviour when choosing non-affiliate demonstrators and simply focusing on positive behaviour or on the lack thereof. By all means, the subordinate observers' choice should be interpreted carefully due to the high variation in the confidence interval.

Effect of rank

Contrarily to our hypothesis, dominant observers showed a preference for the food bowl associated with the lower ranking demonstrator. However, this was only true when both demonstrators were lower ranking. Subordinate observers, too, preferred the bowl on the side of the lower-ranking demonstrator, but when both demonstrators were higher ranking than them. This means that observers chose the lower ranking demonstrator if both demonstrators were in a different rank category than them.

This could be explained when taking the producer/ scrounger model in consideration. Some individuals explore and sample the environment (producers) while others adopt their behaviour or steal their information/ food (scroungers) (Barnard and Sibly 1981). Studies have demonstrated that scroungers are often dominant individuals in a group (Lendvai et al. 2006, Stahl et al. 2001, Werdenich and Huber 2002). A study with barnacle geese (*Branta leucopsis*) showed that for the most part subordinates detected attractive foraging sites, whereas dominant birds displaced them and claimed it for themselves (Stahl et al. 2001). So it may be possible, that the dominant females in this test acted as scroungers and therefore assumed the lowest-ranking individual of their demonstrators to be the producer.

Similar findings are also reported by McCormack and colleagues (2007) in Mexican jays (*Aphelocoma ultramarina*) where the birds evaluated their conspecific's rank and joined lower-ranking birds at a food source. However, the rank-distribution of producer-scrounger roles mentioned before (subordinate producers and dominant scroungers) could not be confirmed (McCormack et al. 2007). Also other studies did not find a connection between hierarchical rank and the role as scrounger or producer (Evans et al. 2021). Similarly, we cannot make this connection, as our test setup was not designed to evaluate the likelihood of an individual to discover a new food source and therefore being labelled a producer. In this study, we were only able to test which traits of demonstrators are likely used by observers to identify them as a valuable producer.

Finally, the fact that both LR and HR observers chose the lowest-ranking individual (when confronted with demonstrators of the opposite rank category) could be explained as stress avoidance behaviour. When measuring the heart rate, dominant macaques and baboons have shown the lowest heart rate within a group. When they were removed, the next dominant animal immediately relaxed as the heart rate decreased (Cherkovich and Tatoyan 1973). Also subordinate Cynomolgus monkeys (*Macaca fascicularis*) were more aggressed and more stressed than dominant monkeys and scanned their environment more often (Shively 1998). This would substantiate the theory that the observers favoured the lowest-ranking demonstrator due to stress avoidance behaviour.

Added to this, the confidence interval should be taken into consideration, too. For subordinate observers the confidence interval showed a less precise prediction in comparison to the dominant ones.

<u>Effect of observation time</u>

In our hypothesis we predicted that the demonstrator which received more attention would get chosen inside the hut. Quite the contrary was observed based on our results: The more a demonstrator was observed, the less likely the observer would have preferred its bowl connected to it.

The reason for going in the opposite direction when having spent more time interacting with one demonstrator could be the potentially obstructed view when positioned on one of the demonstrator's side. Until the end of observation time, the observer spent most of his time interacting with its preferred demonstrator. When the trap door opened, the observer was often positioned completely to the right or left side, so it entered the hut diagonally towards the other demonstrator's side.

Also an observer was considered to give its attention to a demonstrator when either the head or the snout was positioned in the left or right third of its compartment. Of course, the actual span of attention cannot be measured by a simple spatial position of the head and snout, so the viewing direction should have been taken into consideration. Because the camera perspective from above did not allow assessing the pig's line of vision, the head and snout position was the only way to measure the attention span. However, the distance was assumed to play a crucial role in detecting the olfactory cues, that are usually thought of as the most important for pigs. Furthermore, their short vision makes it more likely to visually identify group mates when in closer proximity.

Effect of test number

It was surprising that throughout the tests a change for favouring one side could be observed. Especially since the distribution of demonstrators with regards to rank and RQ was equal between left and right. We assume the bias for the right side with increasing test numbers was not due to unequal demonstrator positions but due to some other factors.

First, the left side was preferred but the increasing test numbers led to a strong tendency for favouring the right side. A possible explanation could be that we slightly changed the setting during the first test round. The first seven tested observers experienced the experimenter leaving the waiting area through the left door (therefore near the left demonstrator, Fig. 2, L), after being led into the observer compartment. In these first seven tests, the majority chose the left side (N=5). To avoid this possible influence in further tests, the experimenter decided to counteract the effect by leaving the waiting area through the middle door (Fig. 2, M) and circuited the hut broadly on the right side. Even though visual covers were shielding the view out of the testing area, and the observer should have therefore not been able to visually follow the experimenter's path, it could have been possible that the observer heard the steps walking by on the right side.

Moreover, the treats (carrots and apples) were placed on the left side of the testing area, whereas the wheat bran was positioned on the right side. The demonstrators often had finished their food troughs when the experimenter arrived with the observer in tow, therefore the troughs had to be refilled. As they were able to watch the experimenter getting the wheat

bran from their right side they might have remembered where it was stored. So when they were in the position to act as an observer they might have recalled their experience as a demonstrator and were possibly drawn towards the right side.
Another possible explanation could be a brain lateralization, which has been found in various species displaying different behaviour with an accentuated preference on a specific side (Camerlink et al. 2018). The domestic cat (*Felis silvestris*) seems to have an individual paw preference when reaching for treats in a testing situation as well as in natural situations when for example stepping over or stepping down (McDowell et al. 2018). In contrast to that, sheep (*Ovis aries*) demonstrated a right-side bias to skirt an obstacle on the level of a population-wise bias (Versace et al. 2007). Lateralization was also found in pigs with a strong bias for curling the tail towards the right side on the population level (Goursot et al. 2018). But to insinuate a lateralization bias towards the left is highly speculative, in particular because the test settings slightly changed after the first seven tests and the choice was nearly balanced during the second and third test.

4.3 Relative observation time

In order to identify whether the demonstrator rank or RQ had an effect on gaining attention from the observer the GLM for relative observation time was fitted. Demonstrator rank was found to significantly affect the observation time, regardless of the observers own rank. Affiliation only played a role in test situations with already very high RQ between the observer and both demonstrators.

Effect of demonstrator rank

When looking at the data for the observation time, an obvious preference for spending time near the subordinate of the two demonstrators was apparent. This effect was true for any combination of observer rank and demonstrator rank. Not only lower ranking observers preferred to spend more time next to the lower ranking of the two demonstrators, but also higher ranking observers were choosing to stand longer next to lower ranking demonstrators. The pigs seem to have a clear picture of the hierarchy when positioning themselves, not only in reference to themselves but also between others. This can also be observed in wild vervet monkeys (*Chlorocebus aethiops pygerythrus*). Here, females seemed to have knowledge of the entire group hierarchy, because reversed playbacks of disputes (a subordinate was the aggressor of a dominant) induced longer periods of looking than “normal” disputes (a dominant harassing a subordinate) (Borgeaud et al. 2013).

Also a highly territorial species of fish (*Astatotilapia burtoni)* not only deduced a linear hierarchy by watching staged fights between five males, they specifically preferred to sojourn with the loser, thus lower-ranking male (Grosenick et al. 2007).

Transitive inference can also be observed in pinyon jays (*Gymnorhinus cyanocephalus*): Within three groups a linear hierarchy was established through staged confrontations (group one: A > B > C > D > E > F; group two: 1 > 2 > 3 > 4 > 5 > 6; group three: P > Q > R > S). One individual of group two (3, the observer) was then removed from his group and watched two encounters, the first between one dominant (A) and one subordinate (B) of a different group than him. For the second encounter, the previous subordinate was now in the role of a dominant (B), while a male above his rank from the observer's own group acted as the subordinate (2). In a staged encounter between the observer (3) and the unfamiliar individual B, the observer reacted submissively, providing evidence that he used transitive inference to predict his own social status (Paz-Y-Miño C et al. 2004).

The Kune Kune females in the present study appeared to have a keen perception of their fellow pigs and decided to stay close to the lower-ranking individual, irrespective of their own rank. A possible explanation could be the reduced stress when lingering near the most subordinate. Hence the question arises whether they are able to spot the lowest-ranking individual within a bigger group of demonstrators and how the males fit into the mould. It would be interesting if they would still spend the majority of their observation time near the subordinate boar rather than a dominant sow.

Furthermore, if the Kune Kune pigs can really use transitive inference for classifying themselves within a small subgroup, further studies could investigate if they are also able to predict their status by watching staged encounters. Such tests could confirm if pigs are able to infer the hierarchical structure of other groups through observation, or if they need own experiences with the respective counterparts in order to form this knowledge about the group hierarchy. This distinction cannot be made with our current test setup as the females of this study all know each other since the day they are born and therefore could have used their own rank to infer about the lowest ranking demonstrator. The one with the least perceived distance in rank could have elicited a stronger reaction in terms of observation time. Of course, for a test conducted like the one with the pinyon jays another sounder of completely unacquainted pigs would be necessary. The realisation would be logistically impossible with the current possibilities at the Haidlhof, but it could easily be tested in conventionally kept pigs in farms, as the piglets do not usually get to know other litters up to the point in time where they are regrouped.

Effect of RQ

In this study, the relative observation time was, as expected, affected by the demonstrator RQ. Observers paired with two demonstrators with an overall high RQ spent more time close to the most affiliate demonstrator.

A playback experiment conducted by Whithouse and Meunier (2020) with Tonkean maqaque (*Macaca tonkeana*) females revealed that a mimicked recording of two affiliates disputing attracted more attention in terms of looking time in individuals rather than hearing non-affiliates. Moreover, when third-party-friendships were also taken into consideration, the individual hearing the recording reacted stronger when having a direct relationship with one of the two subjects. The authors suggested that by paying more attention to "friends", the maqaques stay updated about the current social network within the group or the dispute between friends would be less usual and therefore more interesting (Whitehouse and Meunier 2020).

In our experiment, the observer pigs could have also expected novel and more interesting information from the most affiliate demonstrator and therefore lingered near its compartment.

Moreover, it could be possible that the pigs remember the positive experiences with the most affiliate demonstrator, or observed other pigs interacting in a favourable way with said demonstrator. In a study Luna and colleagues (2021) investigated observational learning through positive interactions with humans. The pigs were divided into three groups, the dominant and subordinate pigs were pooled separately as well as a control group. High-ranking pigs watched a low-ranking demonstrator receiving gentle handling, likewise low-ranking pigs watched a high-ranking demonstrator. Pigs in the control group were only allowed minimal human contact. When each demonstrator was confronted with the human, the demonstrators with an observational experience showed less fear and accepted more stroking than control group pigs. Additionally, they displayed a lower level of stress, measured by the heart rate and heart rate variability. Astonishingly, no difference between low-ranking and high-ranking observers could be detected (Luna et al. 2021).

With these bearings in mind, the Kune Kune females may not have only gained experience by interacting with their conspecifics during the daily life, they could have also collected affiliations by simply watching others. According to our study, if observers interact with demonstrators with an overall low RQ, they tend to prefer the demonstrator with the least RQ. This result should be interpreted with care, because a lot of variation depicted in a broad confidence interval accompanied said outcome.

4.4 Total observation time

As the overall attention might have been impacted by the demonstrators' traits or other effects like the test number, a model for the total observation time was fitted.

Effect of RQ

According to our study, a combined positive RQ resulted in less attention towards the demonstrators. The pigs were looking around more often and were less focused on their conspecifics.

These findings completely contradict our previous results on the relative observation time. It should be expected that the observers show a similar interest in affiliate demonstrators because of the above described reasons. The results for the total observation time are less dependable, because the model estimate is very low, while the standard error is very high, culminating in a low t-value.

But when trying to interpret this less dependable result, it could be possible that the attention was not focused on individuals with a positive RQ, because these individuals may not provide new information. A study from Schwab and colleagues (2008) described this effect in jackdaws, as they preferentially learned from non-affiliated conspecifics. They explain this result with the close proximity of affiliates, which leads to a similar experience of different situations. Non-affiliated individuals are further apart from each other and thus develop different strategies, therefore their informational value increases for distant individuals (Schwab et al. 2008).

Additionally, as pigs with a combined more positive relationship spend more time together, they may not need the full two minutes of exposure phase to base their decision upon. On the contrary, a combined negative RQ may leave them uncertain whose side they should grant more attention and whose food they would eventually eat.

Effect of rank

Our prediction that dominant demonstrators are favoured in terms of total observation time did not apply. Although a slight tendency for LR observers preferring LR demonstrators could be seen, our results were not significant.

Maybe the fences hindered the display of naturally occurring fear of LR observers when confronted with a HR demonstrator. Therefore LR observers could have displayed less fear towards a HR demonstrator than when encountering each other in everyday situations, for example when foraging at the pasture. Because of the fences, they knew from experience that they will not be displaced or threatened and could satisfy their curiosity without fearing the HR demonstrator.

<u>Effect of test number</u>

The more tests the pigs were completing, the more they ignored the demonstrators as the total observation time decreased.

This can be explained by the fact that with increasing test numbers the pigs anticipated entering the hut and getting their reward, even though tests were one week apart each time. They learned that after two minutes in front of the closed door, the door would miraculously open and a delicious treat would await them. When looking through the recordings, the majority was fully engaged in trying to open the door by scratching with their hoofs or by using their snout. Said effect was to be expected, as the Kune Kune pigs have proven to be having a keen perception and fast learning abilities.

4.5 Demonstrator distribution

Regarding the demonstrator distribution, the RQ and rank was equally distributed between right and left side throughout the four test rounds. Any anomalies or undependable results are unlikely to be based on a biased arrangement of demonstrator traits towards one side.

4.6 Side bias counter

As the two-choice test inside the hut was rewarded, the possibility of the pigs developing a side bias for choosing the food bowl was expected. Therefore, the procedure of a side bias counter was executed. The observers needed on average three to four trials to reverse their decision inside the hut, many even needed only one trial at times, reversing instantly.

One study has dealt with the phenomenon that animals refuse to abandon a previously chosen side in subsequent trials: Cattle (*Bos taurus*) being led into a Y-shaped maze experienced either restraint on one side or could walk through the other side undisturbed. Naturally, the majority chose after further trials the unrestraint side. After switching the restraint side to the other side, the animals refused to abandon their previously applied behaviour resulting in experiencing restraint. This effect was even predominate after two weeks (Grandin et al. 1994).

One can conclude from that that we may have successfully worked against a side preference and that the pigs approached each test neutrally. Moreover, the pigs only acted as an observer once a week and in the meantime gained equal experiences from being demonstrators. As demonstrators, they were fed in both compartments since they switched places after the observer left.

The phenomenon of animals avoiding abandoning their previously learned behaviour is called “win-stay” strategy, whereas the opposite is described as “win-shift” strategy. A study by Mendl and colleagues (1997) found out that pigs revisited food areas where they have previously eaten. They interpreted this behaviour as a win-stay strategy (Mendl et al. 1997). A few years later they investigated a predisposition for this strategy and performed tests in a radial arm maze: The 20 male pigs were divided into two groups, where either the win-stay or the win-shift strategy was rewarded. During the course of testing it became apparent that pigs learned the win-shift strategy faster and more accurate, than the win-stay strategy (Laughlin and Mendl 2000). The authors explained the contradiction with different task requirements.

According to our data, the pigs successfully adapted the win-shift strategy by choosing the opposite and previously rejected side on the fourth trial. A study from Roelofs and colleagues (2017) discovered that sows performed better at reversal learning in a spatial holeboard task, as they explored quicker and more hiding places of food. They also decided more frequently to search for food at previously unrewarded places (Roelofs et al. 2017). It would be interesting if the boars showed a similar learning curve than the females and if some boars would reverse instantly, just like some females did.

4.7 Test setting

Although this study provided new and significant insights into the Kune Kune pigs’ behaviour, the test setting could be optimized.

In many behavioural studies with rats involving socially transmitted food preference the demonstrators actively eat the flavoured food (Figueroa et al. 2020, Galef et al. 1988, Galef and Stein 1985, Galef and Whiskin 2001). Galef and Stein (1985) showed that the effect for observers choosing the demonstrator’s diet was weaker when only the rear or a dead rat’s face was powdered with flavoured diet. Surrogates rolled in the same diet induced no preference at all. Although they proved that olfactory cues emitted from the digestive tract or remains of food in the fur were sufficient enough to transmit a food preference, enhanced food preference only occurred when the rat’s breath was present (Galef and Stein 1985).

In a following study Galef and colleagues (1988) identified two components in a rat’s breath, carbon disulfide (CS_2) and carbonyl sulfide (COS) which were only emitted from the nasal cavities. Anesthetized demonstrators were rolled in flavoured food and either dropped with CS_2 or distilled water. Demonstrators which experienced an exposure to CS_2 showed a significantly higher preference for their demonstrator's flavour. On top of this and in contrast to the study in 1985, even surrogates rolled in flavoured food and moistened with CS_2 clearly affected the observer's choice (Galef et al. 1988).

Figueroa and colleagues (2020) conducted a similar experimental setup, although the administration form of the aromas varied: One group of demonstrators was fed with solid aromatized food, the other with aromatized liquids. The observers interacting with demonstrators having eaten solid food chose the flavoured solid food from the demonstrator and could easily transfer their preference when exposed to the same flavour in liquid form. In contrast to that, the transfer from liquid to solid food did not work for observers, which previously interacted with an liquid fed demonstrator (Figueroa et al. 2020). In another study Figueroa and colleagues (2020) proved that social transmission of food preference is also present in pigs (Figueroa et al. 2020).

Bearing these findings in mind and coming back to the present study, it may have not been sufficient to simply spray the demonstrator pigs to induce a preference and the consumption of aromatized food of the demonstrators could have produced clearer results.

Moreover, mouth-to-mouth contact between rats seemed to compensate for a relatively short observation time (two minutes), whereas individuals may need a longer time span if observations take place with distant interactions to have a similar outcome (Galef and Stein 1985). The interaction time in Figueroa's study with pigs also was scheduled with 30 minutes while demonstrators and observers were located in the same pen (Figueroa et al. 2020). The Kune Kune pigs were able to observe each other for merely two minutes and could not interact freely as they were separated by a fence. The fence was not solid, however, and body contact between pigs was, to a degree, possible. Also, if we let them interact in the same pen, like Figueroa and colleagues (2020), lower-ranking observers with high-ranking demonstrators would have shown anxiety and stress reactions towards the high-ranking individuals. This would probably have had the unwanted effect of a hindered interaction phase and thus an unreliable choice inside the hut.

On the other hand, the aromas also provided an additional attribute tied to a demonstrator's identity, due to the fact that the demonstrators were not present inside the hut when the observer was given the choice. Therefore, the aromas provided support and guidance for the tested pig, as it had previously smelled them in association with its demonstrators during the interaction time.

4.8 Conclusion

With this study, we could provide evidence that the attention and the food bowl choice of female pigs was influenced by specific demonstrator traits (rank and RQ). Especially high-ranking individuals acted as predicted when choosing the food bowl associated with the more affiliative demonstrator's side and olfactory cue. The fact that low-ranking observers chose the complete opposite remains debatable and appears to be less reliable. Interestingly, the demonstrator's combined traits seemed to have an impact on the observer's bowl choice, because both dominant and subordinate observers preferred the lowest-ranking demonstrator when both demonstrators were from a different rank category than them.

Furthermore, we found evidence that observers paid more attention to the lower ranking of the two demonstrators, indicating knowledge of their relative ranks. Contrary to our predictions, the more observed demonstrator was not chosen inside the hut, which could be due to the measurement of their attention, as close proximity was measured instead of head direction.

To what extent the application of aromas has helped the testing remains debatable. The spray-on may not have been sufficient when taking the data from the rats' olfactory transmission into consideration. Further studies should adopt the method of feeding the aromatized food in order to gain clearer and more dependable results. Although olfactory cues were only provided as spray-on, the female Kune Kune pigs have proven to be influenced by their demonstrators' traits in decision-making, therefore in following studies the demonstrators have to be chosen with great care. As male and female pigs have different life-styles, future studies should also further investigate if boars react similarly in this kind of test setting or if they prefer other traits to identify valuable demonstrators. Furthermore, the ability of pigs to use transitive interference is an exciting new topic that remains to be fully investigated.

5 Abstract

Animals living in groups experience many advantages, for example when gathering information or learning new behaviour through observing their conspecifics. However, they have to carefully select from whom they copy, as information can be outdated or faulty. For example, horses preferred to learn from observing older and therefore more experienced individuals while ravens copy individuals with whom they have a positive relationship.

Pigs, as highly social animals, form stable hierarchies and different relationships to other members or their group, if given the chance. While adult males live solitary, sows and their offspring live in matriline sounders and have ample opportunity to use information of their group mates. Pigs of mostly very young ages have been shown to use social learning in order to gather information about food locations and 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 whether this is based on their rank or relationship quality. First, dominance order was established with dyadic hierarchy tests, where two pigs competed against each other over a monopolizable food source. For an assessment of their individual relationships towards each other, video recordings were analysed by noting affiliative and agonistic behaviours. After finding suitable demonstrator dyads, differing either in rank or relationship quality to the respective observer, four rounds of two-choice tests were conducted, with one round per week. Different demonstrator dyads were presented to observers in each of the four rounds. Different olfactory cues connected with each demonstrator provided additional enhancement of their individuality. After two minutes of presentation, the observer pig was allowed to enter a test hut and given the choice between two food bowls, which were marked with the olfactory cues connected to the respective demonstrators.

Results indicate that dominant sows preferred, as predicted, the affiliative demonstrator, while subordinates tended to choose the non-affiliative individual. Furthermore, the present study confirmed previous studies where animals could quickly deduce their conspecifics' rank, as observers showed a preference for staying near the relatively lower ranking demonstrator during presentation.

Overall, the study proved that different traits on behalf of the demonstrator affect the behaviour of a tested pig and should be taken into consideration for further tests when carefully selecting potential demonstrators.

6 Zusammenfassung

Ein Leben in der Gruppe bringt Tieren viele Vorteile, zum Beispiel beim Beschaffen von neuen Informationen oder beim Lernen durch Beobachten ihrer Artgenossen. Jedoch müssen sie sorgfältig auswählen, von wem sie Verhaltensweisen kopieren, da die Information sehr schnell veraltet oder fehlerbehaftet sein kann. Pferde beispielsweise beobachten ältere und demnach erfahrenere Artgenossen, während bei Raben der ausschlaggebende Faktor eine gute Beziehung ist.

Schweine, als äußerst sozial agierende Spezies, wenden soziales Lernen an um Informationen über Futterangebote zu bekommen und neue Taktiken für die Futtersuche zu lernen. Während adulte Eber Einzelgänger sind, leben die Sauen und ihre Nachkommen in matriachalen Rotten, formen ähnlich wie Wildschweine unter semi-naturellen Bedingungen stabile Hierarchien und bauen zu ihren Artgenossen verschieden starke Beziehungen auf.

Um zu untersuchen ob Schweine bei Informationen zwischen ihren Gruppenmitgliedern hinsichtlich Rang und der Qualität der Beziehung unterscheiden, wurden in dieser Studie 20 adulte Schweine in vier Durchgängen mit verschiedenen Demonstratoren getestet. Die Hierarchie wurde mittels dyadischer Tests analysiert, wobei zwei Schweine gegeneinander antraten um eine Futterquelle für sich zu beanspruchen. Für die Analyse der Beziehungen zwischen den Schweinen wurden Videos auf affiliative und agonistische Verhaltensweisen untersucht. Nachdem passende Demonstratoren für jedes Schwein gefunden wurden, die sich in ihrem Rang und ihrer Beziehung zueinander unterschieden, wurden die two-choice Tests mit verschiedenen Demonstrator Kombinationen in vier Runden durchgeführt. Zusätzlich wurden die Demonstratoren mit Aromen eingesprüht, um mittels olfaktorischer Reize die Individualität jener hervorzuheben. Nachdem das zu testende Schwein zwei Minuten mit seinem Demonstrator interagieren konnte, hatte es in einer Hütte die Möglichkeit zwischen zwei identen Futterschüsseln mit Futter zu entscheiden, welche mit den Aromen der Demonstratoren verknüpft waren.

Wie vorhergesagt zeigen die Resultate, dass dominante Sauen den Demonstrator, mit dem sie eine gute Beziehung haben, bevorzugen. Weiters bestätigt die Studie, dass Schweine schnell die verschiedenen Ränge abschätzen können, da sie eine Präferenz für den relativ niedrig rangingen Demonstrator aufweisen. Die Studie zeigt, dass verschiedene Merkmale des Demonstrators das Verhalten des Testschweins beeinflussen und demnach bei weiteren Tests eine sorgfältige Auswahl passender Demonstratoren getroffen werden muss.

7 Abbreviations

Dem.	Demonstrator
DS	David’s score
Fig.	Figure
GLM	Generalized linear model
GSP	Good scientific practice
hr	High-ranking
ID	Identification
L	Left
lr	Low-ranking
Nr.	Number
Obs.	Observer
R	Right
RQ	Relationship quality
SS	Sociability score
Tab.	Table

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9 Appendix

Table 14: Excerpt of the live coding sheet for the bowl choice

test.nr	date	time	left.dem	obs	right.dem	choice	comment
1	8.11.	08:25	Zwetschge (lavenderl)	**Beauty**	Zita (jasmine)	r (Z13)	
1	4.11.	12:17	Zita (jasmine)	**Bella**	Zafira (fennel)	l (Z13)	
1	4.11.	11:35	Bibi (lime)	**Bernadette**	Blume (poppy)	r (B6)	
1	4.11.	09:15	Zwetschge (lavender)	**Blossom**	Rapunzel (clove)	l (Z7)	
1	4.11.	10:05	Rosine (mustard)	**Bessy**	Belana (hibiscus)	l (R10)	
1	5.11.	11:45	Beauty (olive)	**Bibi**	Bella (curcuma)	l (B0)	
1	5.11.	12:25	Bessy (parsley)	**Bijou**	Zora (coconut)	r (Z0)	
1	6.11.	09:10	Zora (coconut)	**Blume**	Zafira (fennel)	l (Z0)	
1	5.11.	10:57	Zoe (roses)	**Belana**	Raya (peanut)	l (Z6)	
1	6.11.	09:52	Beauty (olive)	**Rapunzel**	Bijou (sage)	l (B0)	
1	9.11.	08:46	Zwetschge (lavender)	**Rosine**	Zirbe (fir forest)	l (Z7)	
1	6.11.	10:42	Bessy (parsley)	**Rubina**	Raya (peanut)	l (B3)	
1	4.11.	10:50	Bijou (sage)	**Radieschen**	Rubina (vanilla)	l (B5)	
1	3.11.	12:35	Blossom (ginger)	**Raya**	Bessy (parsley)	r (B3)	
1	3.11.	11:30	Blume (poppy)	**Zora**	Bella (curcuma)	l (B6)	
1	6.11.	11:25	Belana (hibiscus)	**Zirbe**	Blossom (ginger)	r (B11)	
1	5.11.	10:23	Rubina (vanilla)	**Zita**	Zafira (fennel)	l (R11)	
1	6.11.	12:05	Bibi (lime)	**Zafira**	Blume (poppy)	l (B4)	
1	8.11.	09:10	Rubina (vanilla)	**Zoe**	Bijou (sage)	r (B5)	
1	9.11.	08:26	Belana (hibiscus)	**Zwetschge**	Zora (coconut)	r (Z0)	

Table 15: Excerpt of the live coding sheet for the side bias. The pigs' side decision during the first round of tests (TestNr 1) on left (l) or right (r) was written down for each trial (1.-10.) After successfully choosing the other side, the food was placed in the middle (m) for two additional trials.

TestNr	Date	Time	ID	1.	2.	3.	4.	5.	5.	7.	8.	9.	10.
1	3.11.	13:00	Z0	l	l	l	l	l	r	m	m		
1	3.11.	13:30	R8	r	r	l	m	m					
1	4.11.	13:20	B11	r	m	m							
1	4.11.	12:55	B3	l	l	l	l	l	l	l	r	m	m
1	4.11.	13:33	R6	l	l	l	l	l	l	r	m	m	
1	4.11.	13:09	B10	r	r	l	m	m					
1	4.11.	13:53	B1	r	m	m							
1	5.11.	13:15	B5	l	m	m							
1	5.11.	13:28	B4	l	l	l	l	r	m	m			
1	5.11.	13:00	B9	l*	l	l	r	m	m				
1	5.11.	13:11	Z13	r	m	m							
1	6.11.	13:11	B6	l	l	r	m	m					
1	6.11.	12:46	R1	l	l	r	m	m					
1	6.11.	13:02	R11	l	l	l	l	l	r	m	m		
1	6.11.	13:22	Z12	l	m	m							
1	6.11.	13:32	Z2	l	l	l	l	r	m	m			

10 List of figures

11 List of tables