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Original Article

Witness for resolution: post-conflict quadratic affiliation in semi-free ranging pigs

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Abstract

In social mammals, post-conflict resolution can involve the reunion of former opponents (reconciliation), spontaneous/solicited post-conflict affiliation of a third party with either opponent (triadic contacts), and affiliation between other individuals (hereafter bystanders; quadratic contacts). Quadratic contacts—possibly informing complex cognitive abilities—have been neglected in post-conflict studies. We investigated quadratic affiliation in semi-free ranging pigs *Sus scrofa*, at the ethical farm Parva-Domus (Cavagnolo, Italy). Kinship was known. We collected behavioral data on adult pigs (n = 104) via video recordings (43 h) followed by video analyses. Affiliative and anxiety behaviors between bystanders were collected under post-conflict (PC; following a conflict between non-bystanders) and matched-control (MC; no conflict) conditions. Quadratic affiliation was present in pigs, as bystanders affiliated more in PC than MC, and such affiliation was followed by a decrease in the anxiety behaviors of both the interacting bystanders. Thus, quadratic contacts may be partly aimed at reducing one's own anxiety (intrinsic regulation). Quadratic affiliation was highest between closely related bystanders, which suggests that such affiliation may be most effective when close kin is involved. Quadratic affiliation was lowest after reconciliation and spontaneous triadic contacts. This suggests that direct peacemaking between opponents and spontaneous triadic contacts with close kin may most likely replace quadratic affiliation. Hence, pigs can be influenced by the negative events that affect other pigs—but not themselves—and their response may be modulated by social factors. Such non-random quadratic affiliation may point toward the presence of elements of social appraisal abilities in pigs.

Key words: anxiety reduction, emotional regulation, reconciliation, social appraisal, triadic contacts.

Group living bears benefits—such as decreased predation chances and increased access to food and breeding mates—but also costs, such as increased competition and inevitable conflict of interest over resources (de Waal 2000; Majolo et al. 2008; Chapman and Valenta 2015). When a conflict of interest emerges between two individuals and takes the form of aggression, the agonistic encounter can negatively affect the whole social group, as it can escalate and potentially lead to group disruption (De Marco et al. 2010; Schino and Sciarretta 2015). To reduce the possible damage deriving from aggression, different post-conflict strategies can be enacted and can involve the "peaceful" reunion of former opponents (*reconciliation*; de Waal and van Roosmalen 1979) or a "friendly" contact between either opponent and an uninvolved third party (*triadic affiliation*; Romero et al. 2009, 2011). In technical terms, reconciliation is defined as the first affiliative contact exchanged between the former opponents occurring in the first minutes following the end of the aggression (de Waal and van Roosmaleen 1979). Reconciliation likely requires individual recognition abilities and implicit memory of previously encountered subjects (Cords and Thurnheer 1993; Aureli et al. 2002) and—by restoring the relationship between former opponents and/or possibly facilitating access to resources—it can work in relieving the anxiety deriving from the conflict (Norscia and Cordoni 2014; Aureli 1997; Silk 2006; Romero et al. 2009; McFarland and Majolo 2011). Triadic affiliation is defined as the first affiliative contact exchanged between an uninvolved third party and either opponent in the first minutes after a conflict (Romero et al. 2009, 2011). Such triadic affiliation can be "*solicited*" if the affiliation with the third party is initiated by a former opponent (de Waal and Aureli 1996; de Waal 2000) or "*unsolicited*" if the third party takes agency in the post-conflict affiliation and spontaneously approaches and contacts one of the former opponents (de Waal and Preston 2017). Solicited affiliation may be involved in intrinsic social regulation (*sensu* Zaki and Williams 2013) as the former opponent initiates a social contact to possibly regulate *its own* experience (Cordoni et al. 2023). Indeed, solicited affiliation can decrease the probability to receive further aggression from other group members (Palagi and Norscia 2013; Palagi et al. 2014) and/or reduce self-anxiety (Palagi and Cordoni 2009; McFarland and Majolo 2012; Puga-Gonzalez et al. 2014). Unsolicited triadic affiliation may require that the individuals initiating it possess elements of social appraisal (sensu Walle et al. 2017) to possibly change their own experience and/or the experience of the contacted subject (intrinsic and/or extrinsic regulation; Cordoni et al. 2023). Unsolicited affiliation can indeed protect the aggression recipient from

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further attacks (Das 2000; Romero et al. 2011; Palagi and Norscia, 2013; Cordoni and Palagi 2015) and reduce its anxiety, in which case the functional term "consolation" is also used (de Waal and van Roosmaleen 1979; Fraser et al. 2008; Fraser and Bugnyar 2010; Romero and de Waal 2010; Palagi and Norscia 2013; Cordoni et al. 2023).

Overall, post-conflict affiliation can reduce the anxiety produced by the aggression in the opponents and/or third parties involved in such affiliation (e.g., de Waal and Aureli, 1997; Fraser et al. 2008, 2009; Fraser and Bugnyar 2010; Cordoni et al. 2023). However, former opponents and third parties are not the only group members that can be affected by aggression because the effect of an aggressive event can reverberate on the entire group and its members, increasing social tension (De Marco et al. 2010). In this respect, the interactions between bystanders can form part of the conflict resolution process. In few studies on primates, it has been observed that uninvolved bystanders simply witnessing an aggression (not taking part as third parties in post-conflict strategies) can increase affiliation contacts between each other after the conflict (Judge and Mullen 2005; De Marco et al. 2010; Daniel and Alves 2015). This type of interaction between bystanders is called *quadratic affiliation*, which is more exactly defined as the first affiliative contact exchanged between bystanders in the first minutes after a conflict (Judge and Mullen 2005). To our knowledge, so far quadratic affiliation has been only reported in primates and specifically in three out of four African monkey species investigated for the presence of the phenomenon, namely Japanese macaques, (*Macaca fuscata*, Daniel and Alves 2015), hamadryas baboons (*Papio hamadryas*: Judge and Mullen 2005), and Tonkean macaques (*Macaca tonkeana*, De Marco et al. 2010) but not geladas (*Theropithecus gelada*, Leone et al. 2010). Interestingly, no quadratic affiliation has been detected in bottlenose dolphins *Tursiops truncatus*, which show both reconciliation and triadic contacts (Yamamoto et al. 2015, 2020). The absence of quadratic affiliation appears to be associated with tolerant species possessing relaxed dominance style, which would make conflicts not so stressful to induce affiliation between bystanders (Leone et al. 2010; Daniel and Alves 2015; Yamamoto et al. 2020).

When present, quadratic affiliation can help bystanders mitigate emotional arousal after witnessing a conflict (Judge and Mullen 2005). Indeed, in the few primate species where quadratic affiliation has been found, such affiliation worked in reducing self-directed behaviors associated to anxiety in the bystanders (hamadryas baboons, Judge and Mullen 2005; Japanese macaques, Daniel and Alves 2015), although not always consistently across groups (Tonkean macaques, De Marco et al. 2010). Hence, as it occurs with other post-conflict strategies, quadratic affiliation may contribute to restoring group homeostasis after a potentially disruptive event. Despite its relevance to group stability, quadratic affiliation has been almost totally neglected in animal post-conflict studies, possibly because it can prove difficult to reliably and comprehensively collect behavioral observations on opponents, third parties and bystanders altogether after a conflict and on a representative sample of agonistic encounters.

In this study, we investigated for the first time the possible occurrence of quadratic affiliation in domestic pigs *Sus scrofa* and specifically in a large mixed sex/breed group raised in a natural grassland-woodland habitat and under semi-free ranging conditions (extensive farming). In such conditions, pigs can express the full array of social behavioral patterns of their wild counterpart (i.e., wild boar; Jensen 1986; Jensen 2002; Stolba and Wood-Gush 1989; Norscia, Collarini et al. 2021). Domestic pigs are good candidates to investigate the phenomenon of quadratic affiliation because they show complex social interactions based on different sensory modalities that include vocalizations and body postures used for inter-individual communication (d'Eath and Turner 2008; Horback 2014) and olfactory behaviors such as nose-to-body and nose-to-nose contacts that are used for social exploration and affiliation (Camerlink and Turner, 2013; Camerlink et al. 2014; Špinka 2017). Moreover, domestic pigs possess advanced cognition, including the ability to identify familiar individuals and items, different post-conflict strategies (reconciliation/triadic contacts), sensitivity to the emotional states of conspecifics, and ability to respond to their distress (Reimert et al. 2013; Marino and Colvin 2015; Reimert et al. 2015; Goumon and Špinka 2016; Camerlink et al. 2018; Norscia, Coco et al. 2021; Norscia, Collarini et al. 2021; Cordoni et al. 2023). Based on the previous framework we formulated the following predictions

Presence of quadratic affiliation (Prediction 1)

Pigs are not always tolerant as they can use repeated aggression to establish ranking positions especially during regrouping and females can form linear hierarchies (Meikle et al. 2010; D'Eath 2002; Andersen et al. 2004; Norring et al. 2019). Aggressive behavior in pigs can have important consequences on animal health as it can alter stress physiology and increase anxiety not only in the opponents by also in other group members (Fernandez et al. 1994; Norscia, Collarini et al. 2021). Moreover, Cordoni et al. (2023) found that pigs are able to engage in different post-conflict affiliation (reconciliation and triadic contacts) to restore group homeostasis. Hence, we expected to find an increase of affiliation between bystanders following a conflict compared to a control condition (*quadratic affiliation*).

Impact of quadratic affiliation on bystander anxiety (Prediction 2)

Previous studies have found that quadratic affiliation can work in reducing self-directed behaviors associated with anxiety in the bystanders (Japanese macaques, Daniel and Alves 2015; hamadryas baboons, Judge and Mullen 2005). Norscia et al. (2021) found that aggression can lead to an increase of anxiety/tension-related behaviors (self-scratching/body rubbing, head/body shaking, yawning, and vacuum chewing) and that the individuals that were not opponents—more than the opponents themselves—expressed the highest rates of such behaviors. Because in pigs conflicts can impact the whole group, we expected that quadratic affiliation would work in reducing anxiety in the bystanders (*Prediction 2a*). Moreover, in pigs spontaneous triadic post-conflict affiliation by third parties can decrease the anxiety in the recipient of an aggression and not in the third party (possibly informing elements of extrinsic emotional regulation; Cordoni et al. 2023). If the same applies to the affiliation between bystanders, we expect that the anxiety levels would be reduced in the contacted subject rather than in the individuals that initiate the affiliation *(Prediction 2b)*.

Individual and social factors modulating quadratic affiliation (Prediction 3)

In pigs, different breeds can show different levels of aggressive social behavior (Breuer et al. 2003, Løvendahl et al. 2005;

Turner et al. 2010) and social organizations of adults can vary depending on the sex, with males most commonly dispersing and females forming stable groups (Stolba and Wood-Gush 1989; d'Eath and Turner 2009; Podgórski, Lusseau et al. 2014; Podgórski Scandura et al. 2014). Despite these differences, we expected to find no differences in quadratic affiliation - if present - between sexes (*Prediction 3a*) and breeds (*Prediction 3b*) because these variables had no influence in other post-conflict behaviors and post-conflict anxiety levels (Norscia, Collarini et al. 2021; Cordoni et al. 2023).

Kinship can highly influence post-conflict behavior (e.g., Cheney and Seyfarth 1989). Previous studies on primates found that that quadratic affiliation did not occur more between kin bystanders (Judge and Mullen 2005; De Marco et al. 2010), even thought in hamadryads baboons *Papio hamadryas* the kin of one opponent was more likely to affiliate with the kin of the other opponent(Judge and Mullen 2005). This result was interpreted as possible "quadratic reconciliation" between kin groups. Pig sociality—especially among females—is based on close kinship (Podgórski, Scandura et al. 2021) and a recent study (Cordoni et al. 2023) found that solicited and unsolicited post-conflict triadic contacts in pigs occurred mostly between former opponents and closely kin-related third parties. Hence—based on pig socio-biology—we expected that quadratic affiliation could be enhanced between kin bystanders and when opponents were closely related to bystanders (*Prediction 3c*).

Reconciliation can help repairing the relationship between former opponents and spontaneous affiliation by a third party can be more effective than solicited affiliation in reducing anxiety in the recipient of aggression, as it occurs in pigs and other species (Fraser et al. 2008; Fraser and Bugnyar 2010; Palagi and Norscia 2013; de Waal and Preston 2017; Cordoni et al. 2023). Third-party affiliation can be used as a substitute for reconciliation to restore group homeostasis after a conflict (Judge 1991; Fujisawa et al. 2006; Palagi and Cordoni 2009). Hence, we expected that quadratic affiliation—as a possible substitute of other post-conflict contacts—may be less frequent when reconciliation and spontaneous triadic contacts occurred after a conflict (*Prediction 3d*).

Materials and Methods

Study group and site

This study was carried out on 104 semi-free ranging adult pigs (7–22 months old) that lived in the same group (54 castrated males and 50 females of three mixed breeds (they were not pure breed because at least one grand-parent belonged to a different breed): Parma Black, Large White, and Piedmont Black). The pigs—individually marked every 4–7 days (during feeding when they grouped together) depending on weather conditions via non-toxic livestock painting spray for individual recognition—were housed at the ethical farm "*Parva Domus*" (Cavagnolo, Turin – Italy) in a woodland natural area of about 13 ha (water available ad libitum; provision of food pellets once/day between 8:30 and 10:30 am: Ciclo Unico P, SILDAMIN®).

Kinship determination

Kinship (close: full/half siblings; weak: others) was known from farmer notes and—for those cases in which kinship was unclear—kinship was confirmed via DNA analyses carried out at the Department of Public Health Sciences and Pediatrics, University of Torino (see Cordoni et al. 2023, for details). Genetic analyses were carried out on 31 pigs (two to three individuals sampled from different sibling generations). DNA was extracted by hair bulbs (gathered during the study period) via QIAmp DNA Investigator Kit (Qiagen; www.qiage n.com) by applying the provider's protocol. 11 autosomic STRs were amplified via multiplex PCR Animal Type Pig PCR amplification kit (http://www.bioty pe.de; Biotype AG, Dresden, Germany). Capillary electrophoresis with SeqStudio system (Thermo Fisher Scientific; www.thermofisher.com) was used to obtain the genetic profile typing. Allele frequencies and kinship index (0.08) were based on a mixed sample of domestic pigs (n = 412), consisting of commercial lines commonly used in the production process (Caratti et al. 2010). The mutation rate for all markers was set at 0.002. For each possible dyad of pigs an unspecific kinship search was performed using Familias 3.1.5 "Blind Search" Module (Kling et al. 2014). Likelihood ratio (LR) was calculated for related individuals (sibling/half-siblings and 1st/2nd cousins), scaled versus unrelated. Relationship was assigned according to the maximum LR value observed among the tested relationships.

Data collection and operational definitions

In the period Jun-Nov 2018 two operators (E.C. and a field assistant) recorded videos (via Panasonic HC-V380/V180 and Sony HDR-PJ240E cameras; 224 videos; 43 h) on conflicts including at least one aggressive pattern (see Cordoni et al. 2023, for the full list and description; $N_{conflicts}$= 86), and during 3-min post-conflict (PC) and matched-control periods (MC; in absence of conflict).

The videos were then analyzed, frame-by-frame or in slow motion, via freeware VLC 3.0.6 and extension Jump-to-Time. Intercoder reliability (Cohen's *k;* McHugh *2012*) was at least 0.81 for aggression, post-conflict affiliation, and anxiety-related behaviors (strong agreement; Cordoni et al. 2023). The Cohen's k value was measured using the R function "cohen.cappa" and libraries "irr" and "psych" (R version 3.5.3). Affiliation patterns extracted from videos included rest in contact, social touching, nose–nose contact, nose–body contact, head-over, and social rubbing (see Cordoni et al. 2023, for the full list and description). Aggressive patterns included lifting, biting, mounting, kicking, pushing, chasing, head-knocking (see Cordoni et al. 2023, for the full ethogram). We defined as 1) opponents: the two individuals directly engaging in a fight; 2) third parties: the individuals not involved in the conflict that after the end of the aggression engaged in unsolicited or solicited affiliative contacts with one (or both) of the former opponents; 3) uninvolved bystanders (hereafter bystanders): the other individuals witnessing the aggression that were not involved in the conflict and in any post-conflict affiliation with either opponent (Figure 1). In the 3-min PC/MC we recorded data on: 1) identity, sex, and breed of opponents, third-parties and bystanders (initiating and receiving post-conflict affiliation); 2) if present, the first affiliative contact that occurred between former opponents (hereafter reconciliation), between a third party and either opponent (solicited and unsolicited triadic contacts), and between bystanders (possible quadratic contacts); 3) time of each of the affiliative contacts listed at the previous point; 4) anxiety-related behaviors (head/body shaking, scratching/body rubbing, yawning, vacuum chewing, *as per* Norscia, Collarini et al. 2021). Supplementary Videos S1 and S2 show affiliation between bystanders after an aggression involving other pigs.

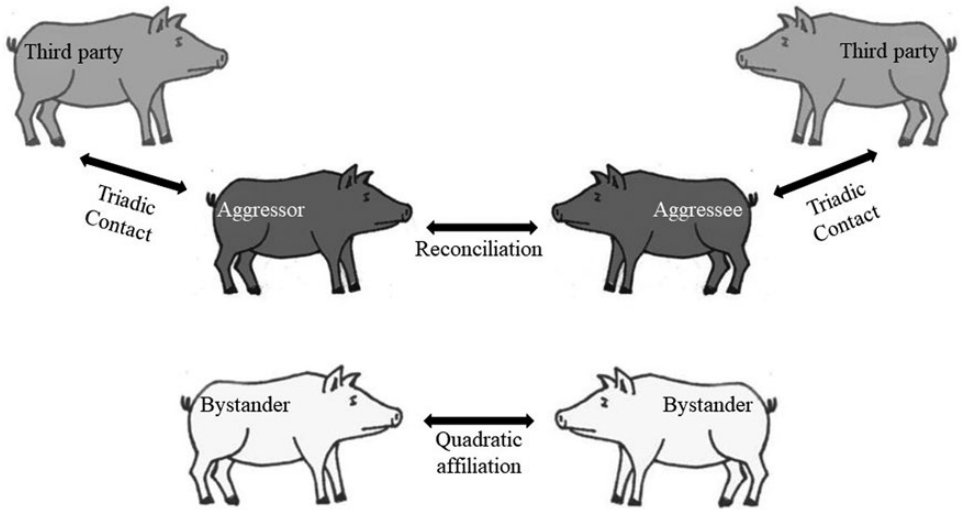

Figure 1. Quadratic contacts within all possible post-conflict affiliation dynamics. Third parties (light gray), bystanders (white) and opponents (aggressor and aggressee; dark gray) are indicated. For the purpose of this study, "bystanders" are those individuals that were not involved in the conflict and in any post-conflict affiliation with either opponent (quadratic contacts). Third parties indicate individuals that were are not involved in the conflict but affiliated with either opponent after the conflict (triadic contacts). Opponents are indicated as aggressor and aggressee, which can also affiliate after a conflict (reconciliation).

A posteriori, we determined the degree of kinship between the bystanders involved in post-conflict affiliation with one another and between each bystander third party that engaged in post-conflict affiliation and either opponent. As per Cordoni et al. (2023), we categorized the kinship as close (half- and full-siblings) and weak (first or second cousins and unrelated individuals).

To evaluate the occurrence of quadratic affiliative contacts we employed the standard PC-MC method used to demonstrate the presence of both reconciliation and triadic contacts in social animals (de Waal and Yoshihara 1983; Arnold and Aureli 2007). After each conflict, we followed bystanders for a 3-min post-conflict period (PC). We employed a 3-min time window as it has been previously demonstrated that in pigs anxiety-related behaviors dropped within such a time window (Norscia, Collarini et al. 2021). For each PC, a corresponding 3-min matched control observation (MC) of the behavior of the same individuals was recorded. MC is usually carried out on a next possible day in the same social (i.e., at least four individuals present to provide the bystander with a similar opportunity to socially interact as in PC; Cordoni et al. 2023) and environmental context (same weather and time ± 1 h) on original bystanders, in absence of aggression in the previous 10 min. We distinguished three types of PC and MC observation pairs with respect to the timing of the first affiliative contact between bystanders: attracted pairs (AP, when the first affiliative contact occurred earlier in PC than MC or only in PC), dispersed pairs (DP, when the first affiliative contact occurred earlier in MC than PC or only in MC), or neutral pairs (NP, when the first affiliative contact occurred in both PC and MC at the same minute or in neither condition). As per de Waal and Yoshihara (1983), the occurrence of quadratic affiliative contacts can be confirmed if the number of attracted pairs is significantly higher than the number of dispersed pairs at the individual level. As for reconciliation and triadic contacts (Veenema et al. 1994), we calculated the individual Quadratic Contact Tendency (QCT%) as follows: ([AP – DP]/[AP + DP + NP]) × 100.

Statistical analyses

The statistical analyses (via SPSS 26.0) were carried out at the individual level and included pigs (N = 49) with at least three PC-MC pairs (which provides the opportunity to have at least one pair/type; Schino et al. 1998).

Owing to normal distribution of contact frequency data (Kolmogorov–Smirnov: P_{males} = 0.109; $P_{females}$= 0.137; $P_{Parma\ Black}$ = 0.200; $P_{Large\ White}$= 0.200), we applied the parametric t-test for two independent samples to compare the bystander contact frequencies between males (N = 28) and females (N = 21) and between Parma Black (N = 27) and Large White (N = 22) breeds. We excluded Piedmont Black individuals because they did not comply with the three PC-MC pairs (minimum) condition.

In case of non-normal data distribution (Kolmogorov–Smirnov with Lilliefors correction: $P \leq 0.001$ for all samples), we also employed non-parametric statistics (Siegel and Castellan 1988). In particular, we applied the Wilcoxon's signed rank test for two dependent samples to compare attracted versus dispersed pairs and assess the presence of quadratic affiliation. Then, we assessed the factors possibly influencing such affiliation and the variation in the level of anxiety of the individuals involved in at least two affiliation contacts with other bystanders (N = 41), so as to ensure the possibility that bystander affiliation could occur in more than one condition. In particular, we applied the non-parametric Wilcoxon's signed rank test for two dependent samples to compare the frequency of affiliation 1) between close and weak kin bystanders; 2) between bystanders that were close or weak kin of either opponent. We used the Mann–Whitney test for two independent samples *via* Montecarlo randomization to check for differences in the level anxiety behaviors between bystanders that initiated affiliation and those that received it. We applied the Friedman's test for $k > 2$ dependent samples to evaluate the potential influence of previous reconciliation contacts (QR), triadic contacts with the aggressee—unsolicited (QUV) and solicited (QSV)—triadic contacts with the aggressor—unsolicited (QUA) and solicited

(QSA)—triadic contacts or no contact at all (QNP) on the probability of observing affiliation between bystanders. We used the same test to assess possible variations in anxiety levels in the absence of quadratic contact (AbsQ), after quadratic contact (PresQ)—both in the initiator and the receiver of the affiliation—and in MC. Because reconciliation, triadic contacts and bystander affiliation could occur at any time within the 3-min PC time window, the frequency of either bystander affiliation and anxiety behaviors were normalized by dividing it by the PC/MC minutes. We applied the Dunn post-hoc test for pairwise comparisons, with the significance level of probability (fixed at 0.05) adjusted downward using the Bonferroni correction.

Results

We found that the attracted pairs were significantly more than the dispersed pairs (Wilcoxon signed-ranks test: N_{pigs} = 49, T = 310.00, ties = 6, P = 0.047; Figure 2). Hence, the phenomenon of quadratic affiliative contacts was present in the pigs under study.

There was a significant variation in the frequency of anxiety-related behaviors across the three conditions (absence of quadratic affiliation, AbsQ; after quadratic affiliation, PresQ; MC; Friedman's test: N_{pigs} = 41, χ^2 = 48.082, df = 2, P < 0.001; Figure 3). Specifically, we detected higher levels of anxiety behaviors in AbsQ than in PresQ (affiliation starting bystanders: Q = 1.037, P < 0.001; affiliation recipients: Q = 1.073, P < 0.001) and in AbsQ than in MC (affiliation starting bystanders: Q = 1.012, P < 0.001; affiliation recipients: Q = 1.049, P < 0.001), whereas there was no difference between PresQ and MC (affiliation starting bystanders: Q = –0.024, P = 1.000; affiliation recipients: Q = –0.024, P = 1.000). We found similar differences in the levels of anxiety behaviors in the bystanders that started the quadratic affiliation (Friedman test: N_{pigs} = 41, χ^2 = 48.515, df = 2, P < 0.001) and in those that received the quadratic affiliation (Friedman test: N_{pigs} = 41, χ^2 = 52.583, df = 2, P < 0.001). The level of anxiety-related behaviors did not differ between bystanders that initiated the quadratic affiliation and bystanders that received it (Mann–Whitney exact test: U = 476.50, $N_{initiator}$ = 32, $N_{receiver}$ = 33, P = 0.301).

No difference in quadratic affiliation frequency was detected between males and females (t-test for independent samples: N_{males} = 28, $N_{females}$ = 21, df = 47, t = 1.121, P = 0.269) and between breeds (t-test for independent samples; $N_{Parma\ Black}$ = 27, $N_{Large\ White}$ = 22, df = 47, t = –1.103, P = 0.277). Quadratic affiliation occurred more frequently between closethan weak-kin (Wilcoxon test N_{pigs} = 41, t = 109.50, ties = 10, P = 0.006; Figure 4a) and was significantly more frequent when the bystanders were closely related to either the aggressor (Wilcoxon signed-ranks test: N_{pigs} = 41, t = 88.00, ties = 3, P < 0.001; Figure 4b) or the aggressee (Wilcoxon signed-ranks test: N_{pigs} = 41, t = 117.50, ties = 2, P < 0.001; Figure 4c).

We found that the likelihood of quadratic affiliation varied across conditions involving the previous presence of different types of post-conflict affiliation (reconciliation, QR; solicited/unsolicited contacts with the aggressee, QSV/QUV; solicited/unsolicited contacts with the aggressor, QSA/QUA) or no previous affiliation (QNP) (Friedman's test N_{pigs} = 41; χ^2 = 65.697; df = 5; P < 0.001; Figure 5). In particular, the pairwise comparisons (via Bonferroni-Dunn post-hoc test)

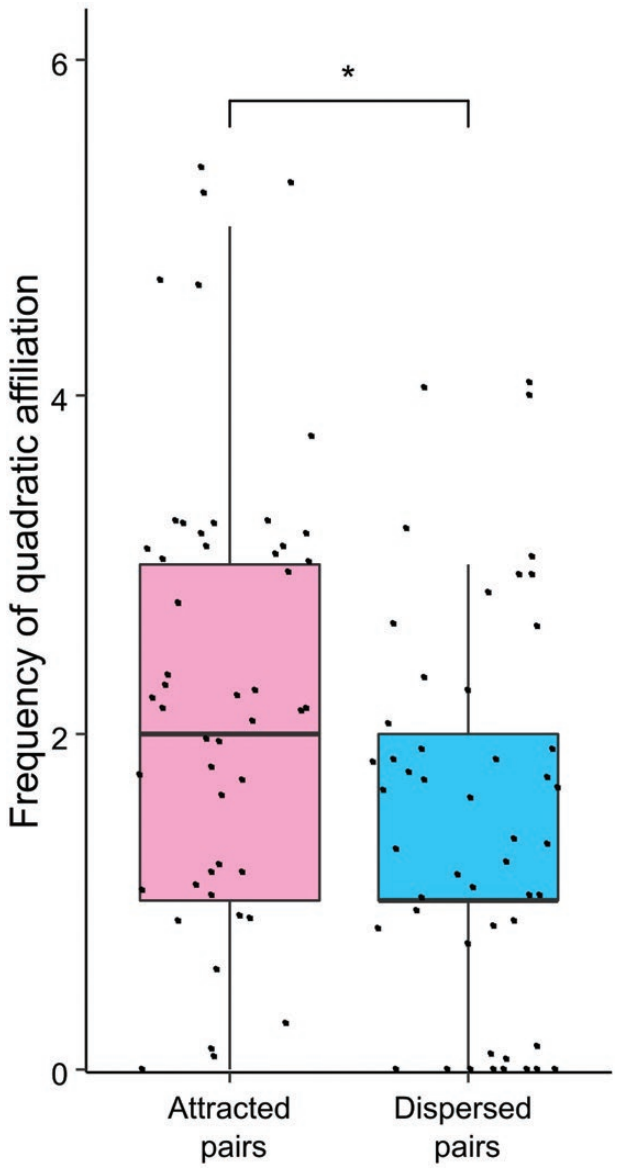

Figure 2. Differences between attracted and dispersed pairs (Wilcoxon signed-ranks test: N_{pigs} = 49, T = 310.00, ties = 6, P = 0.047). Horizontal lines: medians; box length: interquartile range; vertical line: minimum and maximum values in the data; points: data value distribution. NS = non significant; * = P < 0.05.

revealed highest levels of quadratic affiliation (Figure 5): 1) in absence of previous post-conflict affiliation than in presence of unsolicited contacts with the aggressee (Q = –1.841, P < 0.001); 2) in absence of previous post-conflict affiliation than in presence of unsolicited contacts with the aggressor (Q = –1.329, P = 0.019); 3) in absence of previous post-conflict affiliation than in presence of reconciliation (Q = –1.780, P < 0.001); 4) in presence of previous solicited contacts with the aggressee than in presence of unsolicited contacts with the aggressee (Q = –2.024, P < 0.001); 5) in presence of previous solicited contacts with the aggressee than in presence of unsolicited contacts with the aggressor (Q = 1.512, P = 0.004); and 6) in presence of previous solicited contacts with the aggressee than in presence of reconciliation (Q = –1.693, P < 0.001). No difference was found between other conditions (Figure 5). Hence, quadratic affiliation was least likely

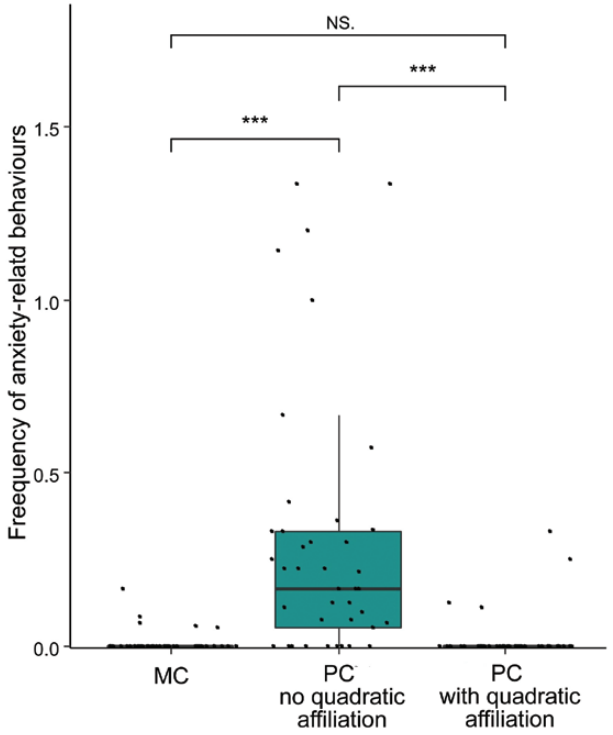

Figure 3. Differences in levels of anxiety-related behaviors across MC, absence of quadratic affiliation and after quadratic affiliation (Friedman's test: $N_{pigs} = 41$, $\chi^2 = 48.082$, df = 2, $P < 0.001$). Horizontal lines: medians; box length: interquartile range; vertical line: minimum and maximum values in the data; points: data value distribution. NS = non significant; *** = $P < 0.001$.

after reconciliation and unsolicited triadic contact toward the aggressee and highest in absence of any previous post-conflict affiliation.

Discussion

Our study shows that quadratic affiliation is present in the domestic pig because individuals not directly involved in aggression as opponents or third party (hereafter bystanders) were significantly more likely to affiliate with one another after witnessing a conflict (PC) than in absence of conflict (MC) (Prediction 1 confirmed; Figure 2). This result indicates that also in pigs—as it occurs in other species—aggressive events can affect the interactions of the entire social group (De Marco et al. 2010; Schino and Sciarretta 2015). As pointed out in the introduction, the domestic pig qualifies as a species in which quadratic affiliation can be adaptive to restore homeostasis as aggression is used to establish or change dominance dynamics that are relevant to the whole group (Meikle et al. 2010; D'Eath 2002; Andersen et al. 2004; Norring et al. 2019). Moreover, in pigs aggression can affect stress physiology and anxiety behaviors—with the latter especially occurring in individuals that are not the opponents—and social affiliation can work in decreasing anxiety (Fernandez et al. 1994; Norscia, Collarini et al. 2021).

We found that quadratic affiliation reduced post-conflict anxiety in the bystanders down to baseline levels (Prediction 2a confirmed; Figure 3). This finding is consistent with the fact that in pigs affiliation (not just quadratic) can accelerate post-conflict anxiety decrease (Norscia, Collarini et al. 2021) and that anxiety in the aggressee can be reduced after a spontaneous affiliation initiated by a third party (Cordoni et al. 2023). This result supports the finding that quadratic affiliation leads to post-conflict reduction of anxiety-related behaviors in the bystanders, as observed in Japanese macaques (Daniel and Alves 2015), hamadryas baboons (Judge and Mullen 2005) and one group (out of two) of Tonkean macaques (De Marco et al. 2010). Depending on how it is expressed, quadratic affiliation might require that a bystander appreciates the emotional behavior of another bystander toward a shared referent (in our case the conflict) and enacts subsequent regulatory mechanisms (elements of social appraisal, as per Walle et al. 2017). Such behavioral mechanisms may reduce the divergence between the bystander actual internal state and its prediction of the other bystander's emotional state and possibly change its own experience (intrinsic regulation) or the experience of the contacted subject (extrinsic regulation) (Zaki and Williams 2013; Prochazkova and Kret 2017; Walle et al. 2017; Cordoni et al. 2023). Our results show that the bystanders that initiated the quadratic contact showed comparable levels of anxiety behaviors as the bystanders that received such contact, which was followed by a decrease of anxiety behaviors in both affiliation initiators and recipients (Prediction 2b not confirmed). An explanation for this result is that the anxiety reduction experienced by the affiliation recipient may be a byproduct of the quadratic contact enacted by the initiator to reduce its own anxiety (intrinsic regulation; *sensu* Zaki and Williams 2013). However, we cannot exclude that elements of extrinsic regulation (Zaki and Williams 2013) underlie quadratic contacts, which also change the emotional state of others (i.e., anxiety reduction in the bystander receiving the affiliation). Consistently, it has been observed in pigs that the unsolicited triadic affiliation that a third party engage with the aggressee can work in reducing the anxiety in the aggressee and not in the third party (Cordoni et al. 2023). Of course, more of a parsimonious explanation may be that quadratic affiliation in pigs is a mere automatic reaction to a stressor (the conflict). However, in the pigs under study, quadratic affiliation was not distributed randomly across group members because it was influenced by kinship (Figure 4) and previous post-conflict affiliation (Figure 5), which may point toward some elements of social appraisal, required also when pigs engage in different types of non-random post-conflict triadic affiliation (Cordoni et al. 2023).

Indeed, we found that quadratic affiliation was affected by kinship because affiliation occurred most frequently between close kin (Figure 4a) and when either opponent was close kin of bystanders (Figure 4b,c). Kinship with the opponents appeared to be one possible driver of quadratic affiliation in hamadryas baboons, even though non-kin of both opponents could engage in such affiliation at comparable rates (Judge and Mullen 2005). Social proximity between bystanders—more than kinship—enhanced their quadratic affiliation in monkeys (hamadryas baboons, Judge and Mullen, 2005; Tonkean macaque, De Marco et al. 2010). This finding can be explained in the light of the social organization of feral pigs and wild boars. Under wild conditions, adult males tend to disperse but sows form social groups of variable size that are based on close kinship (for both males and females) and, in general, the dispersal patterns are reflected in the kin-based social organization (Stolba and Wood-Gush 1989; d'Eath and Turner 2009; Podgórski, Lusseau et al. 2014; Podgórski, Scandura et al. 2014). Hence, social closeness can

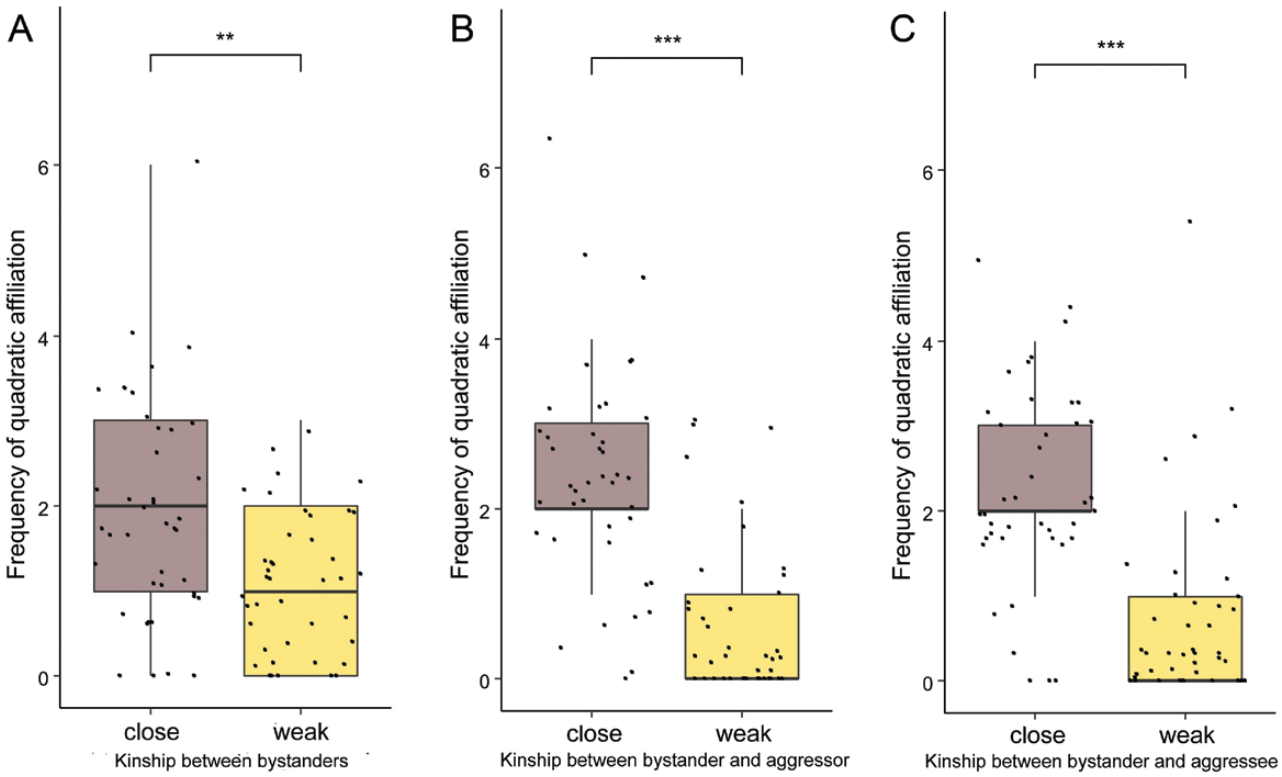

Figure 4. Box plot showing that: (A) quadratic affiliation occurred more frequently between close- than weak-kin (Wilcoxon test N_{pigs} = 41, t = 109.50, ties = 10, P = 0.006); (B) quadratic affiliation was significantly more frequent when the bystanders were closely related to the aggressor ((Wilcoxon signed-ranks test: N_{pigs} = 41, t = 88.00, ties = 3, P < 0.001); (C) quadratic affiliation was significantly more frequent when the bystanders were closely related to either the aggressee (Wilcoxon signed-ranks test: N_{pigs} = 41, t = 117.50, ties = 2, P < 0.001). Horizontal lines: medians; box length: interquartile range; vertical line: minimum and maximum values in the data; points: data value distribution. ** = P < 0.01, *** = P < 0.001.

be associated with close kinship in pigs, at least in the wild. There is evidence, although limited so far, that pigs can recognize kin after separation (McLeman et al. 2005). The involvement of close kin as opponent in the conflict or as partner in quadratic affiliation probably makes such affiliation more relevant to the inclusive fitness of the bystander, as it has also been observed that triadic contacts in the same pig population occurred especially between close kin (Cordoni et al. 2023).

Another non-random aspect of pig quadratic affiliation is that in our sample such affiliation was less likely to occur after reconciliation or unsolicited triadic affiliation toward the aggressee whereas it was most likely in absence of any previous post-conflict affiliation or after solicited triadic contacts toward the aggressee (Figure 5). Contacts initiated by a bystander toward the aggressor did not change the probability of observing quadratic affiliation (Figure 5). These results suggest that quadratic affiliation may come into play as a substitute for other post-conflict behaviors. It is possible that when the conflict is resolved directly by the opponents, via peacemaking, group homeostasis is restored and quadratic affiliation is not required. Reconciliation can work in reducing the anxiety (measured via self-directed behaviors) especially in the aggressee (e.g., domestic goats, *Capra hircus*: Schino 1998; macaques, *Macaca* spp: Aureli et al. 1989; Kutsukake and Castle 2001) but also in the aggressor (e.g., hamadryas baboons: Romero et al. 2009) even though in tolerant species anxiety reduction may not be an issue (e.g., crested macaques *Macaca nigra*: Duboscq et al. 2014). Importantly, in hamadryas baboons—where the phenomenon of quadratic affiliation is present (Judge and Mullen 2005)—witnessing reconciliation can reduce anxiety in the bystanders (Judge and Bachmann 2013). In the same pig population, Cordoni et al. (2023) found that only unsolicited triadic contacts toward the aggressee reduced anxiety in the recipient of the affiliation. Hence, also in this case the adaptive value of quadratic affiliation may be reduced, which may explain why quadratic contacts plummeted when third parties spontaneously affiliated with the aggressee. On the other hand, Cordoni et al. (2023) also found that contacts initiated by a bystander toward the aggressee did not decrease their anxiety whereas solicited contacts with the aggressor after a conflict did not differ from chance (hence such contacts were not elicited by the aggression per se). These previous findings (Cordoni et al. 2023) may explain why quadratic affiliation was not affected by these types of post-conflict behaviors and probably remained necessary to restore group homeostasis.

Finally, sex and breed did not influence the likelihood of such affiliation (Predictions 3a and 3b confirmed), despite the fact that different breeds can diverge in the level of aggressiveness (and related implications), and that males and females show different social organisation as adults, with males usually dispersing and females forming kin-bonded groups (Breuer et al. 2003; Podgórski, Lusseau et al. 2014; Podgórski, Scandura et al. 2014). However, the pigs of our study group were not pure breed and males were castrated. Thus, possible inter-breed or inter-sex differences—if present—may have been reduced under the detection level. Consistently, a previous study on the same population found no sex or breed dependent differences in the anxiety-related behaviors expressed after conflict (Norscia, Collarini et al. 2021).

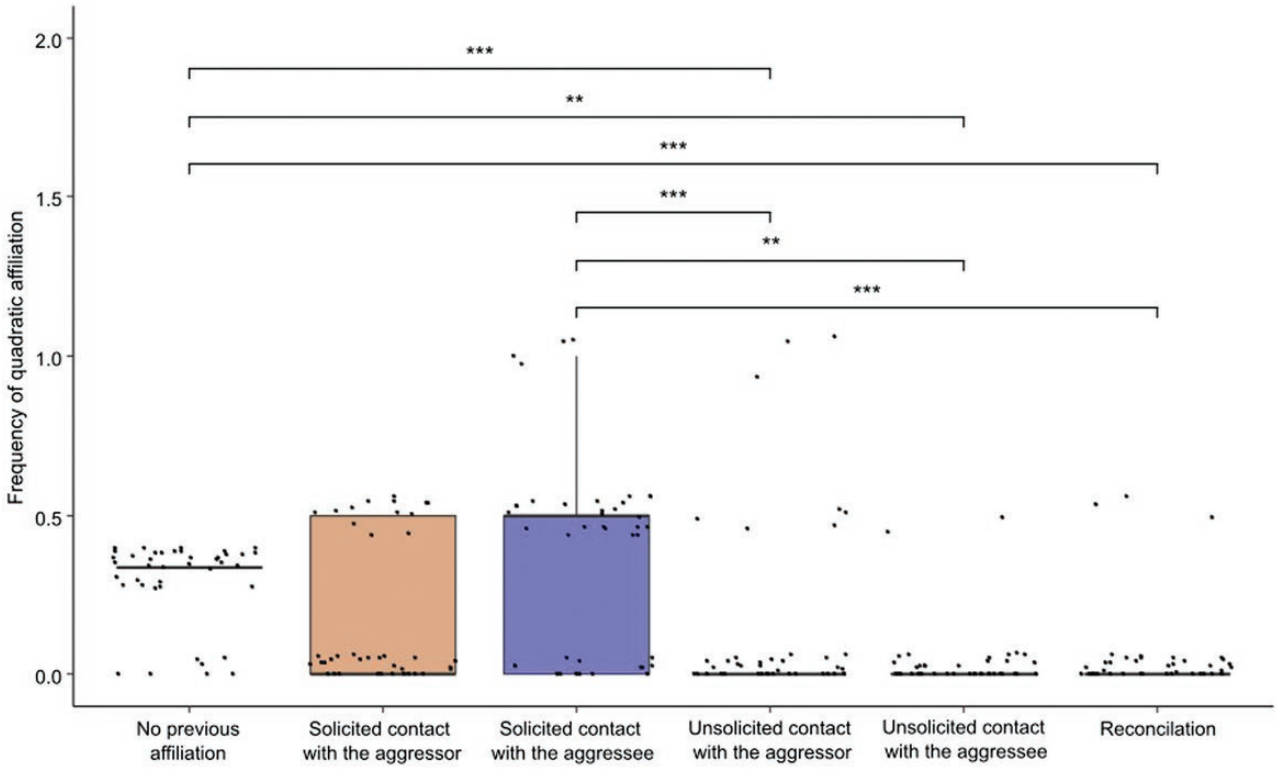

Figure 5. Differences in levels of quadratic affiliation across different conditions involving the previous presence of different types of post-conflict affiliation (reconciliation, QR; solicited/unsolicited contacts with the aggressee, QSV/QUV; solicited/unsolicited contacts with the aggressor, QSA/QUA) or no previous affiliation (QNP): 1) QNP than in QUV (Q = −1.841, $P < 0.001$); 2) QNP than QUA (Q = −1.329, $P = 0.019$); 3) QNP than QR (Q = −1.780, $P < 0.001$); 4) QSV than QUV (Q = −2.024, $P < 0.001$); 5) QSV than QUA (Q = 1.512, $P = 0.004$); 6) QSV than QR (Q = −1.693, $P < 0.001$). No difference was found between other conditions (QUV vs. QR, Q = 0.061, $P = 1.000$; QUV vs. QUA, Q = −0.512, $P = 1.000$; QUV vs. QSA, Q = −0.902, $P = 0.434$; QR vs. QUA, Q = −0.451, $P = 1.000$; QR vs. QSA, Q = −0.841, $P = 0.626$; QUA vs. QSA, Q = −0.390, $P = 1.000$; QSA vs. QNP, Q = −0.939, $P = 0.346$; QSA vs. QSV, Q = 1.122, $P = 0.099$; QSV vs. QNP, Q = 0.183, $P = 1.000$). Horizontal lines: medians; box length: interquartile range; vertical line: minimum and maximum values in the data; points: data value distribution. NS = non-significant; ** = $P < 0.01$, *** = $P < 0.001$.

In conclusion, this study showed for the first time that quadratic affiliation is present in domestic pigs and that - as it occurs for triadic contacts (Cordoni et al. 2023) - it is not randomly distributed across individuals. The main limit of this study is that males were castrated—possibly affecting testosterone levels (Raeside et al. 1997)—and individuals were mixed breed which may have reduced the effect of some individual factors on quadratic affiliation. Hormonal correlates would also be useful to assess stress levels in relation to conflict and subsequent affiliation. Future studies could focus on these aspects but while breed differences may be assessed in multibreed extensive farming, it may prove difficult to reliably collect biological samples for hormonal essays before and after different types of post-conflict affiliation without perturbing the animals and to find multiple reproductive males coexisting in association with female groups. Despite these constraints, we can hypothesize that quadratic affiliation in pigs might not just be a mere response automatically generated by the aggression. Quadratic affiliation led to the reduction of anxiety behaviors in both the interacting bystanders (affiliation initiator and recipient) which suggests that such affiliation is more self- than other-oriented. The fact that quadratic affiliation was not randomly distributed across bystanders but it was modulated by kinship and previous post-conflict behaviors (which may or may not have restored group homeostasis) suggests—as an important evolutionary convergence with primates—that further cognitive processes may be in place, such as elements of social appraisal that can enhance the benefits that a subject obtains by engaging in the affiliation (i.e., own anxiety reduction).

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Author Contributions

Conceptualization, G.C. and I.N.; methodological approach, G.C. and I.N.; data collection and sort-out: E.C.; formal analysis, I.N. and E.C.; genetic analyses: C.R., E.Ch;

writing—original draft preparation, I.N., G.C. and E.C.; writing—review and editing, I.N., G.C. and E.C.; funding acquisition, I.N. All authors have read and agreed to the published version of the manuscript.

Conflict of Interest

The authors declared that they have no conflict of interest to this work.

Ethical Statement

The study—purely observational with no manipulation whatsoever—did not require ethical approval. This study was conducted in accordance with the Italian law Dlg. 4/2014 n. 26 (based on European provisions), which regulates the use of animals in experimental and scientific research. This study is part of the broader project "So.Pig" (Department of Life Sciences and Systems Biology, University of Turin) and PhD PON project "GreenPig" co-funded by the Ministry of University and Research (MUR). These projects focus on domestic pigs that are not raised in a natural environment, with the aim of better understanding social dynamics and their relationship with welfare, the effect of domestication on behavior, best management practices, and possible evolutionary divergences and convergences with other social species, including humans. The subjects under study were reared on an ethical farm (Parva Domus, Turin, Italy) and were housed in a 13 ha enclosure that were parts of a natural woodland/grassland habitat. The pigs were able to move freely and avoid each other if wanted. The study did not require the pigs to be removed from their group either temporarily or on a longer-term basis. Periodically, a vet visited the pigs for vaccination or health problems. We took all possible precautions to avoid any fear, distress or harm on the pigs and to reduce the impact of our presence on their environment. We did not interact with the pigs, which were free to perform their usual maintenance and social activities.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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