


## ORIGINAL RESEARCH

# Examining the effect of sociodemographic factors on feral horses' social networks

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## Keywords

agonistic behaviours; feral equids; grooming; proximity; strength centrality; social networks; social cohesion.

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## Abstract

The benefits of sociality are not equitably shared among members of a social group. The position individuals occupy in social networks is key to maximizing their fitness and contribution to group cohesion, as well as stability in the network structure. Individuals' position in a social network is highly influenced by intra-group competition and affiliation; therefore, it should be assessed by examining various spatial-social variables. In this study, we examined the relationship between proximity, grooming and agonistic networks, controlling for genetic relatedness, and the effects of sociodemographic factors on the strength centrality (SC) of these social networks. We combined drone technology and social network analysis to test several hypotheses on 16 feral horse (*Equus ferus caballus*) groups during three consecutive breeding seasons. Our results show a clear relationship between spatial and social behaviours, suggesting that proximity and grooming are intimately connected in promoting social bonding, and agonism may be a consequence of close proximity between conspecifics. Sociodemographic factors shaped the three network centralities differently. Females and higher-ranking individuals are more central in spatial networks, whereas younger ones may benefit from higher centrality in affiliative networks. Newly integrated individuals tend to be peripheral on spatial networks and engage more in agonistic behaviours; corroborating that integration into a new group is a costly process for females, ultimately leading to a decreased foaling rate. Individuals in multi-male groups showed higher SC in proximity, but not in agonistic networks, suggesting that a second male may play a role in decreasing overall intra-group competition. Our results provide a step forward in understanding the costs and benefits of network centrality in non-matrilineal societies and mechanisms leading to social cohesion, namely in populations under the constant threat of predation and human pressures.

## Introduction

Life in social groups consists of cost–benefit trade-offs and it is only achievable when and if the benefits of sociality outweigh its costs. Those benefits consist primarily of improving individuals' foraging strategies, reducing predation risk, and facilitating information transfer (Ashton et al., 2019; Galef & Giraldeau, 2001; Krause & Ruxton, 2002). Conversely, costs are often linked to an increased risk of disease and parasite transmission, as well as competition for resources (Loehle, 1995; Rasa, 1989; van Schaik & van Noordwijk, 1986). Evidence shows that the costs and benefits of group living are not shared equitably among group

members and the position that each individual occupies in the network is elemental to maximizing their fitness (Krause, 1994; Krebs & Davies, 2009; Rubenstein, 1978). Individuals' position in a social network is highly influenced by their relationships with other group members through intra-group competition and affiliation; therefore, it should be assessed by examining various spatial-social variables (Canteloup et al., 2021).

Predator avoidance and intra-group competition are considered key factors determining the major costs and benefits of spatial position, ultimately shaping the evolution of animal social systems (Sterck et al., 1997; van Schaik & Janson, 1988; van Schaik, 1989; Vehrencamp, 1983; Wrangham, 1980).

Hamilton (1971) proposed the 'selfish herd' hypothesis, which states that the presence of neighbours reduces the risk of predation, consequently individuals at the periphery of the group are under higher predation pressures as they have fewer neighbours. Conversely, higher centrality may entail greater exposure to intra-group competition (Farine & Sheldon, 2015; Oh & Badyaev, 2010). According to the 'food competition hypothesis', while occupying more central positions in the group, individuals are less likely to find food patches or have less access because the resources can be quickly depleted (Hirsch, 2007). In addition to ecological factors, individuals' spatial position in the group network is highly influenced by their relationship with other group conspecifics and individuals' attributes (Hirsch, 2007). For instance, in several animal taxa, dominant individuals tend to occupy more central positions (primate species: Robinson, 1981; Ron et al., 1996; van Schaik & van Noordwijk, 1986, spiders: Rayor & Uetz, 1990, birds: Clifton, 1991; Flynn & Giraldeau, 2001, fishes: Krause, 1994). Sex is also reported to influence spatial positioning, with females being more central than males, the latter being responsible for group protection (primates: Hall & Fedigan, 1997; Janson, 1990; Ron et al., 1996, horses: Inoue et al., 2019). Ontogeny influences intra-group spatial position as well, with juveniles being more prone to occupy central positions (Janson, 1990; Rhine et al., 1981). This age-class difference might arise because of the greater risk of predation faced by younger individuals and the reliance on adults for vigilance and protection (Janson & van Schaik, 1993).

Individuals occupying central positions in affiliative networks may take full advantage of the benefits of group living, thus increasing their long-term reproductive success (Formica et al., 2012; McDonald, 2007) and occasionally their longevity (Silk et al., 2010). Contrastingly, central positions have been linked to greater risks of infectious disease and parasite transmission (Hamede et al., 2009; MacIntosh et al., 2012). Similar to spatial networks, interactions between individuals do not occur randomly and are shaped by sociodemographic factors (e.g. sex, age, kinship, philopatry and rank: Silk et al., 2006; Smith et al., 2002; Wiszniewski et al., 2010). Previous research in primates has shown that higher-ranking individuals are more central in both grooming and agonistic networks (Błaszczuk, 2018; Seyfarth, 1980; Wooddell et al., 2019, but see: Borgeaud et al., 2017). One explanation for the higher centrality of dominant individuals in grooming networks is that grooming can be traded for coalitionary support in agonistic interactions (Seyfarth, 1977; Seyfarth & Cheney, 1984) and tolerance at feeding sites for subordinate individuals (Barrett et al., 1999). Ontogeny affects individuals' network position as well because younger individuals tend to be less central than adults in agonistic networks and have higher centrality in affiliative networks (Shimada & Sueur, 2018; Sosa, 2016; Turner et al., 2018; Wooddell et al., 2019).

Feral horses (*Equus ferus caballus*) live in multi-level societies and establish long-term bonds among intra-group conspecifics similar to other social mammals (horses: Maeda, Ochi, et al., 2021; Maeda, Sueur, et al., 2021; hyenas, *Crocuta crocuta*: Smith et al., 2007; elephants, *Loxodonta africana*: Archie et al., 2006; primate species: Silk, 2007, Stanley et al., 2018).

However, unlike other species, feral horses do not live in matrilineal societies (primates: Silk, 2007; dolphins, *Tursiops aduncus*: Wiszniewski et al., 2010) and their bonds are not determined by kinship (Mendonça et al., 2021). This makes them a good model to explore benefits and costs associated with network position, and test hypotheses relative to affiliation and competition in non-matrilineal societies.

The goals of this study were twofold. First, we examined the relationship between three different social behaviours: proximity, grooming and agonistic behaviours. Proximity and grooming are measures of affiliation among group members, and, in many species, they have been reported to function as a mechanism to establish and maintain group cohesion and social bonds, ultimately increasing individuals' reproductive success (Cameron et al., 2009; Silk, 2007; Snyder-Mackler et al., 2020). Conversely, agonistic behaviours are indicators of intra-group competition, that potentially involve risks of injury and are often linked to decreased reproductive success (Berger, 1986; Cameron et al., 2009; Duncan, 1992). The relationship between grooming and proximity is not consistent across studies because proximity is not always positively associated with grooming behaviour (horses: Inoue et al., 2018; Roberts & Browning, 1998; Shimada & Suzuki, 2020; Sigurjónsdóttir et al., 2003, primates: Arseneau-Robar et al., 2018; Crofoot et al., 2011; Schino & Alessandrini, 2015). It is hypothesised that proximity between conspecifics could be the result of either individual initiatives (e.g. grooming) or passive acceptance (van Dierendonck et al., 2004). If a positive relationship is found between proximity and grooming, then either proximity is likely a result of grooming or, grooming is the result of keeping proximity in a passive way. However, if no relationship is found between the two behaviours, then maintaining proximity is likely an outcome of passive acceptance, or have other social functions (e.g. support against conspecifics and predators, reconciliation). Furthermore, close proximity between individuals may increase the need to obtain and defend space to be able to perform daily activities, which has been reported in previous studies to be the main function of aggression (Heitor et al., 2006; Shimada & Suzuki, 2020). Hence, we predicted a positive correlation between dyadic agonistic interactions and proximity. Previous studies have hypothesised that grooming and agonism comprise examples of reciprocal altruism (Schino, 2007). If a positive correlation is found between agonism and grooming, our results may hint at a reconciliatory mechanism in feral horses (Cozzi et al., 2010, but see: Shimada & Suzuki, 2020). Genetic relatedness has been suggested to possibly affect intra-group affiliation/cooperation and competition, explicitly among females; therefore, in this study, we controlled for genetic relatedness to test the aforementioned predictions (Hex et al., 2021).

Second, we further examined the effects of age-sex class, rank, tenure and group type (one- vs. multi-male group) on the centrality of the three different networks, as well as the relationship between network centrality and female foaling success. On the basis of the hypothesis outlined above, we formulated several predictions about the effect of sociodemographic factors on network centrality:

Using proximity as a proxy for spatial networks, we predicted that (1) higher ranking individuals would be more central, considering that this population is exposed to predation pressures, supporting the selfish herd hypothesis (Hamilton, 1971); (2) males would be more peripheral, as they are responsible for group protection against harassment and predation, a result of their social system – female defence polygyny (Berger, 1986); (3) young individuals would be more central as they may rely on adults for vigilance and protection (Janson & van Schaik, 1993); (4) recently integrated individuals would be more peripheral as a consequence of the integration process; and (5) single-male groups would be more socially cohesive, therefore, a positive effect on spatial networks should be yielded (Linklater *et al.*, 1999).

For grooming networks, we predicted that (1) high-rank individuals would be more central, as grooming can be traded for feeding tolerance and social support (Seyfarth, 1977); (2) adult females would be more central than males, as bonds between females are linked to higher reproductive success and reduced aggression from males (Cameron *et al.*, 2009; Nuñez *et al.*, 2015); (3) younger individuals would be central, as well, if they were to benefit from higher-rank support, whilst allowing them to improve their social skills required for integration into a new group (Monard & Duncan, 1996); (4) individuals with higher tenure would be more central, as higher tenure reflects social stability in horses (Mendonça *et al.*, 2022); (5) single-male groups would yield higher values of strength centrality for grooming networks, as they are expected to be more socially cohesive.

For agonistic networks, we predicted that (1) rank would not have any effect on centrality, since the direction of agonism was not considered (to allow comparisons with other non-directional networks—proximity and grooming), (2) adult females would be the main source of intra-group competition, as female intra-competition for resources is conspicuous in horse societies (Rubenstein, 1994), (3) young individuals would not have higher centrality in agonistic networks, if a central position in the group confers protection against other conspecifics and tolerance, (4) recently integrated individuals would be more central in the agonistic networks, as female integration into a new group is costly and destabilizes the dominance hierarchy (Nuñez *et al.*, 2014); (5) there would be a higher level of agonism in two-male groups compared to single-male groups, as females in multi-male groups receive more aggression than their counterparts in single-male groups (Linklater *et al.*, 1999).

## Materials and methods

### Study site and population

The studied Garrano population inhabited Serra d'Arga (SA, 825 m a.s.l.), a mountain range comprising an area of 4493 hectares in the northwest of Portugal (8°42' N, 41°48' E), characterized by a Mediterranean climate with Atlantic influences. Horses in SA are not managed under the traditional husbandry system; nonetheless, some horses in this population are privately owned and removed by livestock farmers.

Furthermore, this Garrano population is subjected to predation pressures by Iberian wolves (*Canis lupus signatus*; Nakamura *et al.*, 2021). Research on this population has been ongoing since 2016 (Go *et al.*, 2020; Inoue *et al.*, 2018, 2020; Maeda, Ochi, *et al.*, 2021; Maeda, Sueur, *et al.*, 2021; Mendonça *et al.*, 2020, 2021, 2022; Pinto & Hirata, 2020; Pinto *et al.*, 2022; Ringhofer *et al.*, 2017, 2020). Thus far, 35 harem groups and approximately 200 individuals have been identified, including foals (Mendonça *et al.*, 2022).

### Behavioural observations

We collected data between 8:30 h and 19:00 h daily during the breeding seasons (BS) of 2018, 2019 and 2020 (May–August in 2018, May–July in 2019, and July in 2020), totaling 288 h for 16 horse groups (Table 1). We observed the horses on foot from a distance of 5–10 m without evidence that the animals were disturbed. One to six groups were observed for 1 h per day and observations were distributed evenly across the groups and hours of the day. During a 1-h group focal sampling session, mutual grooming and agonistic events were documented using an all-occurrence sampling method, and all individuals were recorded continuously with a video camera (Sony HDR-CX500V, Japan). One observer dictated the behaviours and names of the individuals to the camera to facilitate future video coding. Simultaneously, another observer took aerial photos using an unmanned aerial vehicle (drone, Mavic PRO, DJI, China) to further examine horses' intra-group inter-individual distances (Fig. 1).

Together with behavioural observations, we collected faecal samples to determine the genetic relatedness between individuals. The protocol for DNA extraction, markers, genotyping, and selection of the best estimator is described in the Appendix S1 and reported in Mendonça *et al.* (2021).

All applicable international, national, and institutional guidelines for the care and use of animals were followed. The field observations complied with the guidelines for animal studies in the wild issued by the Wildlife Research Center of Kyoto University, Japan.

### Social behaviours and ranks

Mutual grooming was defined as reciprocal coat care where two partners stand beside one another, often head-to-shoulder or head-to-tail, and groom each other's neck, mane, rump or tail by gently nipping, nuzzling or rubbing (McDonnell, 2003). In total, we recorded 171 mutual grooming events.

Agonistic behaviours included displacements, mild threats, bite threats, kick threats, bites, kicks with the hind legs, and strikes with the forelegs (McDonnell, 2003). In total, we coded 2303 (out of 2364) agonistic behaviours that elicited a submissive response (avoidance or withdrawal), for rank determination. We built group-based winner/loser matrices and determined an individual's rank using David's Score (DS) (David, 1987) in the 'steepness' R package (de Vries *et al.*, 2006). To allow comparison between different groups, we standardized DSs using the following formula:

**Table 1** Summary of the data on the composition, observation time and total drone scans for each focal group in a herd of feral horses (*Equus ferus caballus*) in Serra d'Arga, Portugal

Breeding season	Group name	Group size	N males	N females	Young individuals <sup>a</sup>	Hours observed <sup>b</sup>	Total of drone scans
2018	Gozen&Nagaoka	5	2	3	0	8	46
	Hakata	5	1	3	1	12	72
	Harajyuku	8	1	6	1 (dis)	10 (12)	50
	Hitachi	6	1	3	2	8 (12)	51
	Kamakura&Zama	6	2	4	0	6 (10)	34
	Kitakami	8	1	7	0	10	67
	Kobe	9	1	7	1	8	60
	Nanba&Tennoji	7	2	4	1 (dis)	9 (11)	46
	Takaoka&Uozu	5	2	2	1	10	59
	Total	59	13	39	7	81	485
2019	Aso	3	1	2	0	13	98
	Daisen	5	1	3	1 (dis)	9	63
	Gozen&Nagaoka	4	2	2	0	15	94
	Hirosaki	5	1	4	0	13	66
	Nanba	6	1	5	0	13	80
	Seki	4	1	3	0	13	92
	Takaoka&Uozu	5	2	2	1	14	89
	Toki	5	1	2	2	9	60
	Unnan	6	1	4	1	13	77
	Total	43	11	27	5	112	719
2020	Aso	6	1	5	0	14	78
	Daisen	6	1	3	2 (dis)	13	68
	Gozen&Nagaoka	5	2	2	1 (dis)	12	93
	Hirosaki	5	1	4	0	15	74
	Takaoka&Uozu	5	2	2	1	15	87
	Toki	4	1	2	1	13	81
	Unnan	6	1	4	1	13	87
	Total	37	9	22	7	95	568
2018–2020	Total	3–9	19	55	13	288 (300)	1772

Groups are named after the male or males of the group. dis = individuals that have joined the group by dispersal.

<sup>a</sup>Individuals between 1 and 4 years of age; young individuals consist of 12 young females and only one young male belonging to Hitachi group.

<sup>b</sup>Numbers within parenthesis correspond to the number of hours the group was followed; numbers outside parenthesis correspond to the number of hours used in the analyses. Data were excluded for groups whose composition changed during the targeted breeding season as a result of the integration or disappearance of group members.

$$DS_i' = \frac{DS_i - DS_{\max}}{DS_{\max} - DS_{\min}}$$

where the  $DS_i$  values ranged from 0 to 1 for each individual (0 corresponding to the most subordinate and 1 to the most dominant individual).

### Spatial data: inter-individual distances and proximity

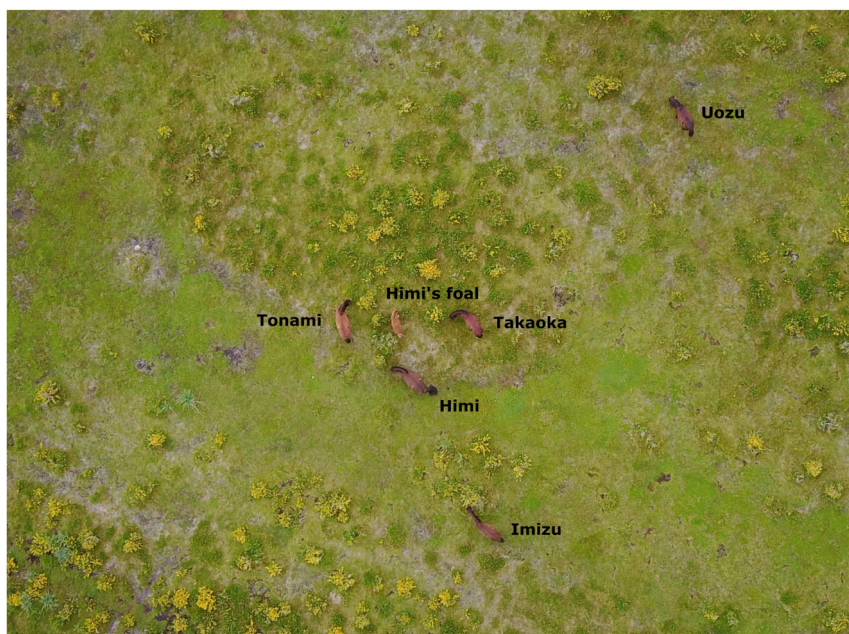
We used a drone to take aerial photos of each focal group. To avoid data pseudoreplication, we set the scan interval for the capture of aerial photos at 10 min (Christensen et al., 2002; Feh, 1988). We analysed the aerial photos following the protocol developed by Inoue et al. (2018) to determine inter-individual distances using body lengths (BL) as a unit measurement (details in the Appendix S1). The proximity between individuals in a

group was defined as being within 3 BL of one another (Mendonça et al., 2021). In total, we analysed 1772 photos, ranging from 3 to 7 photos taken per hour (Table 1).

### Social network analyses

To estimate the strength of association between two individuals, we used measures of frequencies for proximity, grooming and agonistic behaviour. All the agonistic interactions analysed were unidirectional; however, to allow comparison with non-directional matrices (proximity, grooming), we considered the total of interactions that occurred within a dyad to calculate the frequencies. We calculated simple ratio indices (SRIs) for each behaviour to normalize the data across different groups. SRIs were used because all individuals were present throughout the observations (Hoppitt & Farine, 2018). The SRI was defined as follows:





**Figure 1** Aerial photo taken with the drone of Takaoka&Uozu—a two-male group—in 2018 ( $n = 5$ ); each aerial photo corresponds to a scan.

$$\text{SRI} = \frac{x}{x + y_a + y_b}$$

where  $x$  represents the frequency of proximity (scans in proximity/h), grooming or agonistic behaviours (events/h) between individuals  $a$  and  $b$ ,  $y_a$  is the frequency of these behaviours between individual  $a$  and other individuals, and  $y_b$  is the same as  $y_a$ , but for individual  $b$  (Cairns & Schwager, 1987). In addition, we calculated a distance index (DI) from the mean distance between each pair of individuals:

$$\text{DI} = \frac{D_{ab} + 0.5 (D_a + D_b)}{0.5 (D_a + D_b)}$$

where  $D_{ab}$  represents the mean distance between individuals  $a$  and  $b$ , and  $D_a$  and  $D_b$  represent the maximum distance between individuals  $a$  and  $b$  and other individuals, respectively. Thereafter, we obtained four dyadic weighted indices of behavioural factors (distance, proximity, grooming, and agonistic interactions) ranging from 0 to 1 (Table S1). The DI and proximity SRI were used to examine the relationship between proximity and distance, as well as a proxy to characterize the spatial positions of individuals within the group (Inoue *et al.*, 2018). The SRIs were used to calculate SC for different social networks (proximity, grooming, and agonistic behaviours).

### Matrices and network attributes

We built 25 matrices for each type of interaction (25 for proximity, 25 for grooming, and 25 for agonistic events) with the values obtained from the SRIs. We organized matrices per group and per BS, corresponding to 16 groups over three BS (nine groups in the BS of 2018, nine groups in the BS of

2019, and seven groups in the BS of 2020), because the group composition changed from a year to another (see Table 1). From the generated matrices, we calculated the node strength centrality, defined as the sum of the weights assigned to the node's direct connections (strength centrality – SC), using the 'ANTS' R package (Sosa *et al.*, 2020) (Table S1). We opted to use SC as a measure of network centrality as opposed to, for example, the eigenvector of centrality (which considers both the connections to the node and its alters) because when dealing with small networks both metrics are almost identical. Moreover, SC provides a more direct interpretation of the results – the stronger the adjacent connections to a node, the more central the node is.

For each individual, we determined a value of SC for the three consecutive breeding seasons. The values of SC were standardized (SC') using the following formula:

$$\text{SC}' = \frac{\text{SC}_i - \text{SC}_{\max}}{\text{SC}_{\max} - \text{SC}_{\min}}$$

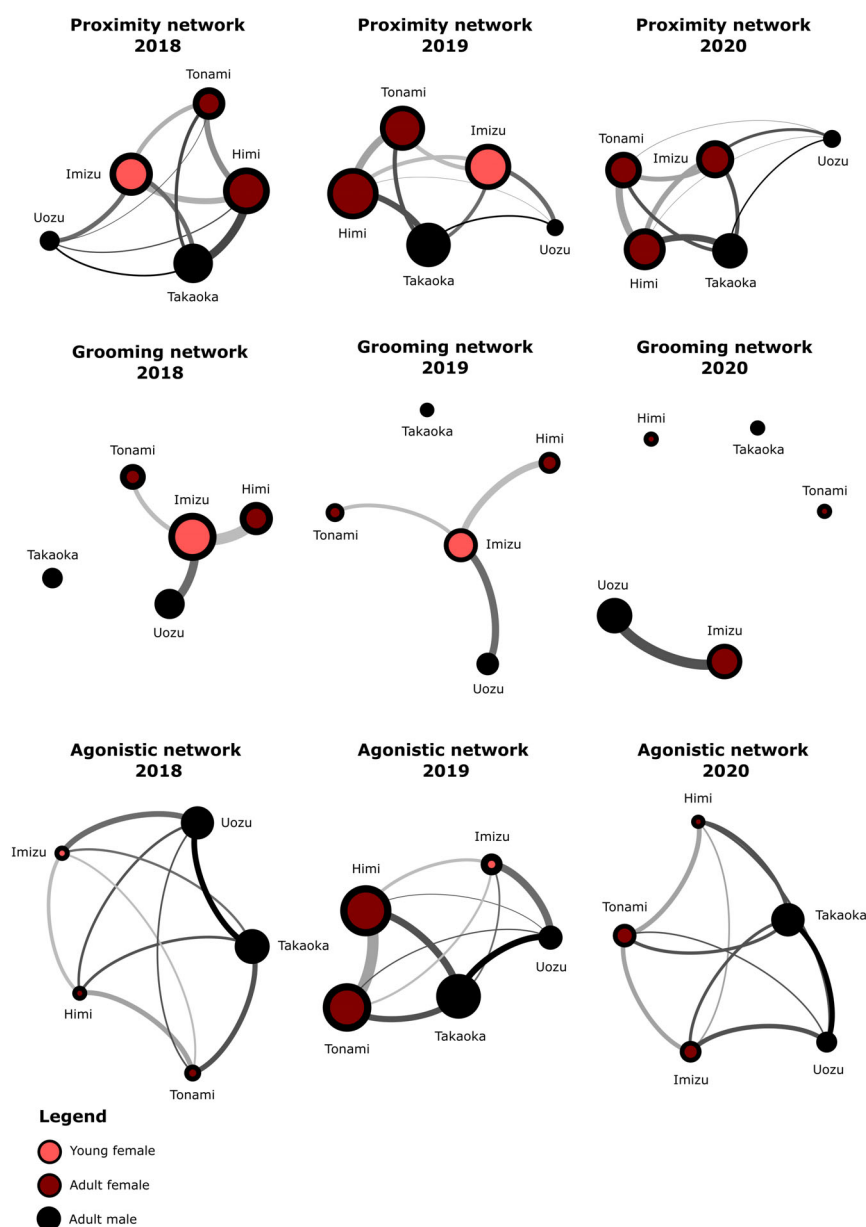
where the SC' values, that is, normalized SC, ranged from 0 to 1 for each individual (0 corresponding to the least central and 1 to the most central individual in the networks). To simplify, from here on, SC' will be referred to as SC.

### Examining the relationship between matrices

We used the R code provided by the 'ANTS' R package (Sosa *et al.*, 2020) to conduct node-level permutations ( $n = 10\,000$ ) on 25 different matrices constructed with DIs and SRIs from proximity, grooming, and agonistic matrices, before conducting regression analysis. We built four generalized linear mixed models (GLMMs) with a Gaussian structure to examine the

relationship among multiple-group SRI matrices. Firstly, we examined the relationship between two spatial matrices—inter-individual DI matrices and SRIs derived from proximity matrices. To assess the relationship between different multi-group matrices (proximity, grooming and agonistic behaviours), we then built three different GLMMs using the SRIs derived from intra-group dyads for the three different interaction matrices controlling for genetic relatedness. One model was built to assess the relationship between proximity and grooming, with the proximity SRIs as a fixed factor. The second model assessed the relationship between proximity and the agonistic

SRIs, with the proximity SRIs as a fixed factor. Finally, we investigated the relationship between agonistic behaviours and grooming with a third model, using agonistic SRIs as a fixed factor. In all models, genetic relatedness was incorporated as a fixed factor. We included the identification (ID) of both individuals involved in the interaction, group ID, and BS as random factors. In all models, permutations were restricted within the grouping variable 'group ID' to control for location biases. An example of the three social networks (proximity, grooming and agonistic) is shown in Fig. 2 for the Takaoka&Uozu group.



**Figure 2** Example of social networks for Takaoka&Uozu, the only group that kept the same social composition throughout three breeding seasons. Networks were built using the program Gephi 0.9 and the Force Atlas layout. The size of the node corresponds to the individual's strength centrality (SC) value in the respective network; the edges' thickness represents the value of the simple ratio index.

Since we are dealing with relatively small group networks ( $n < 10$ )—a characteristic of feral horses' groups—there is a probability for models ran with 'ANTs' R package to return unstable regression estimates. To assure that this is not the case for our dataset, we conducted repeated permutations to examine the reliability of the estimates retrieved for all regression models (Tables S3–S5).

### Effect of sociodemographic factors on network SC

Before conducting regression analysis, we conducted 10 000 node label permutations using the 'ANTs' R package. The post-network permutation analyses consist of swapping the pairs of nodes to obtain randomized networks from shuffled group affiliations (Croft *et al.*, 2011; Sosa *et al.*, 2021). Three GLMMs with a Gaussian structure were built to investigate how SC in the proximity, grooming, and agonistic networks were affected by different factors: age-sex class (male, female, young), rank (0–1), tenure (established and new) and group type (single-male and multi-male groups). Horses were classified according to their sex and age-class as adult females, adult males (>4 years old) and young individuals (>1–<4 years old). Regarding tenure, horses were classified as 'new' in the group if they were observed for the first time in the BS that the observation took place, and 'established' if the horse had been observed for at least 1 year in the same group (Mendonça *et al.*, 2021). Interactions between factors were included when yielding a significant effect in the model. In all models, we tested 87 individuals and 16 groups in the BS of 2018 to 2020 and included individual ID, group ID, and BS as random factors. In all models, permutations were restricted within the grouping variable group ID.

### Effect of SC and sociodemographic factors on female foaling success

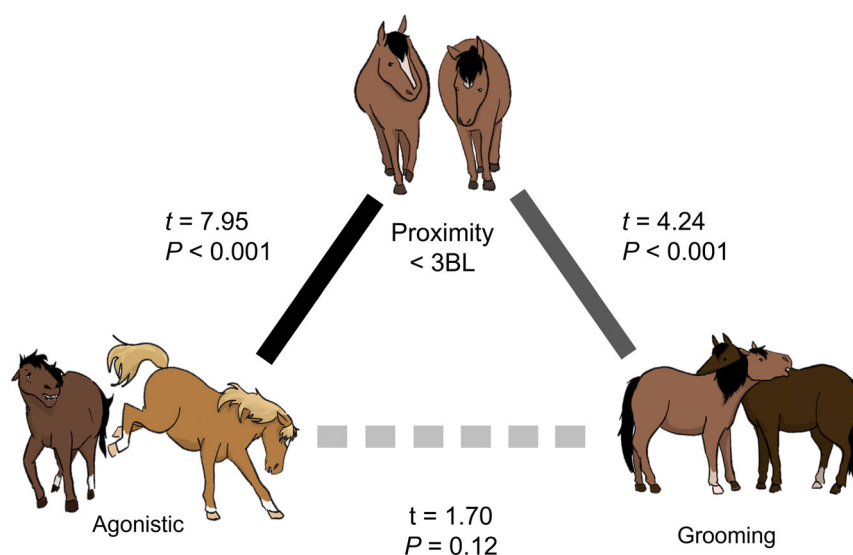
To investigate the effects of network centrality on foaling success, we built a GLMM logit link function with a binomial error structure (females that foaled in the next breeding season were scored as 1, and females that did not foal were scored as 0). Proximity SC and agonistic SC, as well as social factors, such as rank and tenure, were included as fixed effects. For the foaling success models, we included only groups where at least one of the females foaled. We excluded the season of 2018–2019 when foal mortality reached 100% within the first month of life (Mendonça *et al.*, 2022). Consequently, we predicted the foaling success in the subsequent breeding seasons of 22 adult females. Individual ID was included as a random factor. We did not consider the effect of grooming SC due to the high correlation with proximity SC, and because, excluding the data from 2018 from the analyses resulted in even fewer events.

## Results

### Relationships between matrices

For conciseness, we present only the results concerning proximity, grooming and agonistic networks. The results on the relationship between inter-individual distances and proximity can be found in the Appendix S1.

A positive effect was found for proximity matrices on grooming (GLMM:  $t = 4.24$ ,  $P < 0.001$ , Fig. 3, Table S2) and agonistic matrices (GLMM:  $t = 7.95$ ,  $P < 0.001$ ) when controlled for genetic relatedness. Genetic relatedness had a positive effect on grooming (GLMM:  $t = 2.62$ ,  $P = 0.01$ ).



**Figure 3** Results of the generalized linear mixed models (GLMMs) evaluating the relationship between matrices (proximity, grooming and agonistic). The relationship is stronger between agonistic and proximity matrices, indicated by the black line and grooming and proximity matrices, indicated by the dark grey line. The dashed grey line indicates that no significant effect was found between grooming and agonistic matrices. Significance was set as  $P < 0.05$ .

Nonetheless, genetic relatedness did not affect agonistic behaviours (GLMM:  $t = 0.11$ ,  $P = 0.82$ ). Moreover, no relationship was found between grooming and agonistic behaviours (GLMM:  $t = 1.70$ ,  $P = 0.12$ ).

### Effect of sociodemographic factors on SC

Males tend to have lower SC in proximity networks; that is, they are more spatially peripheral compared to adult females (GLMM:  $t = -8.04$ ,  $P < 0.001$ , Table 2, Fig. 4a) but no difference was found between adult females and younger individuals (GLMM:  $t = 0.99$ ,  $P = 0.25$ , Table 2). Rank showed a positive effect on proximity SC; higher-ranking individuals are more central in the proximity network (GLMM:  $t = 4.31$ ,  $P < 0.001$ , Table 2, Fig. 4b). Group type had a significant positive effect on proximity SC; multi-male groups tend to have a higher proximity SC compared to single-male groups (GLMM:  $t = 3.72$ ,  $P < 0.001$ , Table 2, Fig. 4c).

The age-sex class had a significant effect on grooming SC in the grooming network; young individuals tended to engage in grooming more frequently than adult females (GLMM:  $t = 2.45$ ,  $P = 0.01$ , Table 2, Fig. 5a), and no difference was found between adult females and males (males, GLMM:  $t = 0.91$ ,  $P = 0.36$ , Table 2). Tenure showed only a marginal effect on grooming SC (GLMM:  $t = 1.56$ ,  $P = 0.08$ , Table 2, Fig. 5b).

Age-sex class (male, GLMM:  $t = -6.06$ ,  $P < 0.001$ , Table 2, Fig. 6a), tenure (established, GLMM:  $t = -3.20$ ,  $P = 0.02$ , Table 2, Fig. 6b) yielded a significant effect on

agonistic SC. Group type showed a positive marginal effect (multi-male group, GLMM:  $t = -1.55$ ,  $P = 0.05$ , Table 2, Fig. 6c). The interaction between age-sex class and group type also showed a significant effect in the agonistic SC model (group type (multi-males): class (male): GLMM:  $t = 4.06$ ,  $P < 0.001$ , Table 2, Fig. 6c).

In the foaling success model, female tenure was the only factor that showed a significant effect on foaling success (GLMM,  $z = 2.82$ ,  $P = 0.03$ , Table 3).

### Discussion

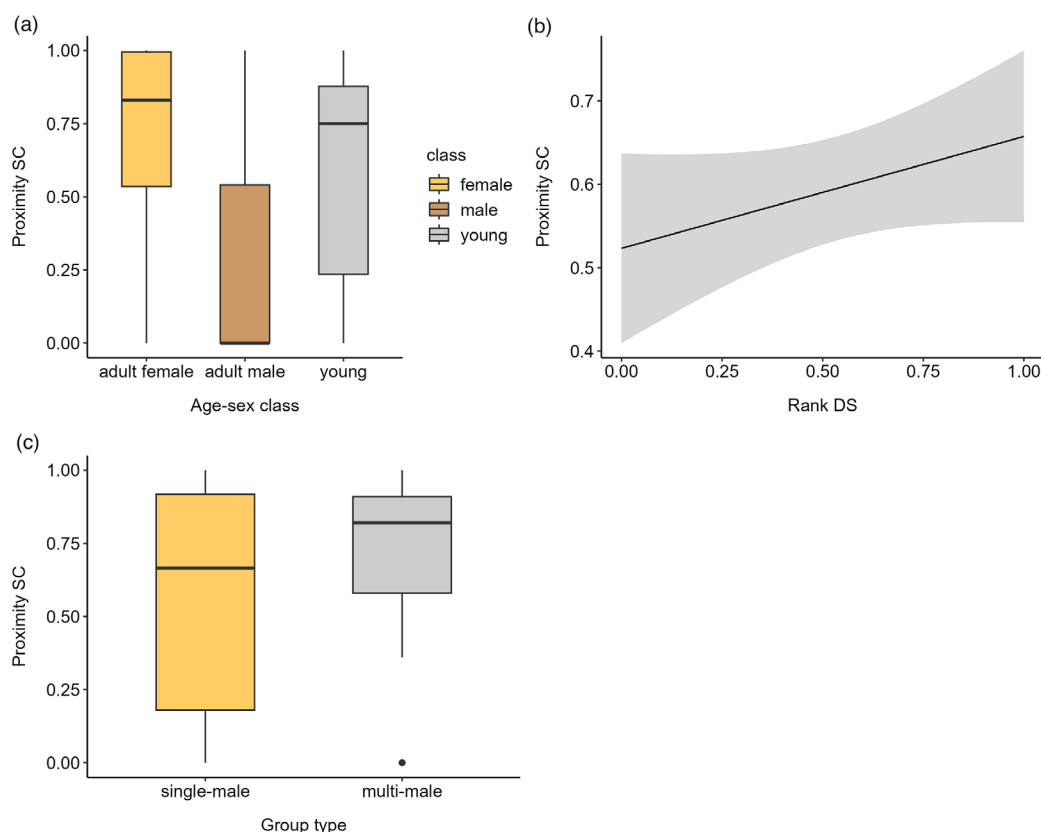
Our results highlight a positive relationship between proximity and grooming networks which supports the hypothesis that proximity is an active process, rather than a result of passive acceptance, in this feral population (van Dierendonck *et al.*, 2004). A positive relationship was also shown between agonistic behaviours and proximity, strengthening the premise that agonistic interactions may be a by-product of the spatial proximity between conspecifics (Granquist *et al.*, 2012; Heitor *et al.*, 2006; Shimada & Suzuki, 2020). Grooming behaviour has been reported to strengthen affiliation between conspecifics (primates: Dunbar, 1991; Lehmann *et al.*, 2007; Silk, 2007; feral horses: Cameron *et al.*, 2009; plains zebras, *Equus quagga*: Tong *et al.*, 2015). Considering that grooming occurred mostly in pairs that were close in proximity (Sigurjónsdóttir *et al.*, 2003; van Dierendonck *et al.*, 2004), our results support the role of grooming as a precursor mechanism to strengthening intra-group affiliation in feral horses. No

**Table 2** Summary of statistics for three separate generalized linear mixed models (GLMMs) investigating the effects of age-sex class, tenure, rank and group type on strength centrality (SC) of proximity, grooming and agonistic social networks of feral horses (*Equus ferus caballus*) in Serra d'Arga, Portugal

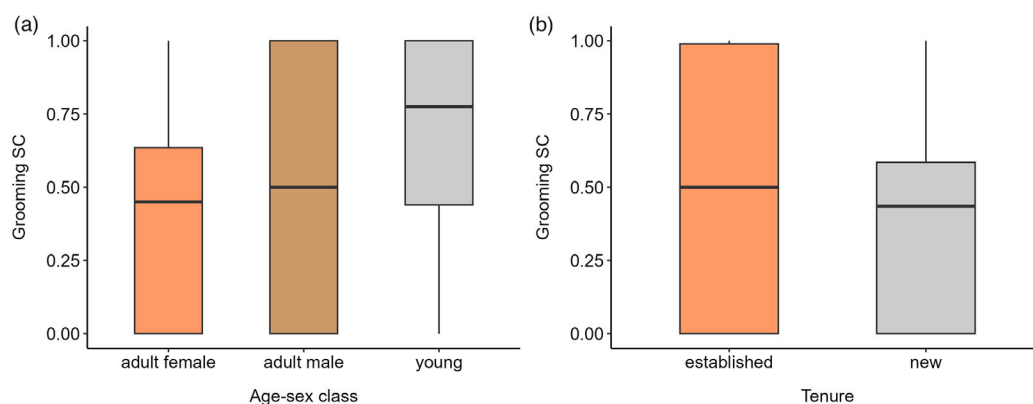
Response variables	Fixed effects	Estimate	SE	<i>t</i>	<i>P</i>
SC proximity network	(Intercept)	0.42	0.07	5.77	0.04
	<b>Class (male)</b>	-0.56	0.07	-8.04	< <b>0.001</b>
	Class (young)	0.09	0.09	0.99	0.25
	Tenure (established)	0.05	0.06	0.90	0.50
	<b>Rank DS</b>	0.36	0.08	4.31	< <b>0.001</b>
	<b>Group type (multi-male)</b>	0.23	0.06	3.72	< <b>0.001</b>
SC grooming network	(Intercept)	0.27	0.09	2.86	0.00
	Class (male)	0.08	0.09	0.91	0.36
	<b>Class (young)</b>	<b>0.27</b>	<b>0.11</b>	<b>2.45</b>	<b>0.01</b>
	Tenure (established)	0.12	0.08	1.56	0.08
	Rank DS	0.13	0.11	1.19	0.19
	Group type (multi-male)	-0.08	0.08	-1.06	0.24
SC agonistic network	(Intercept)	0.87	0.08	10.73	0.00
	<b>Class (male)</b>	-0.56	0.09	-6.06	< <b>0.001</b>
	Class (young)	-0.17	0.11	-1.55	0.15
	<b>Tenure (established)</b>	<b>-0.21</b>	<b>0.07</b>	<b>-3.20</b>	<b>0.02</b>
	Rank DS	-0.01	0.09	-0.10	1.00
	Group type (multi-male)	-0.14	0.09	-1.55	0.05
	<b>Group type (multi-male): Class (male)</b>	0.60	0.15	4.06	< <b>0.001</b>
	Group type (multi-male): Class (young)	0.00	0.20	0.01	0.94

GLMMs included individual ID, group ID and breeding season as random effects. Significance is set at  $P < 0.05$  and significant fixed effects are highlighted in bold. *P*-value (*P*) is calculated based on permutations ( $n = 10\,000$ ).





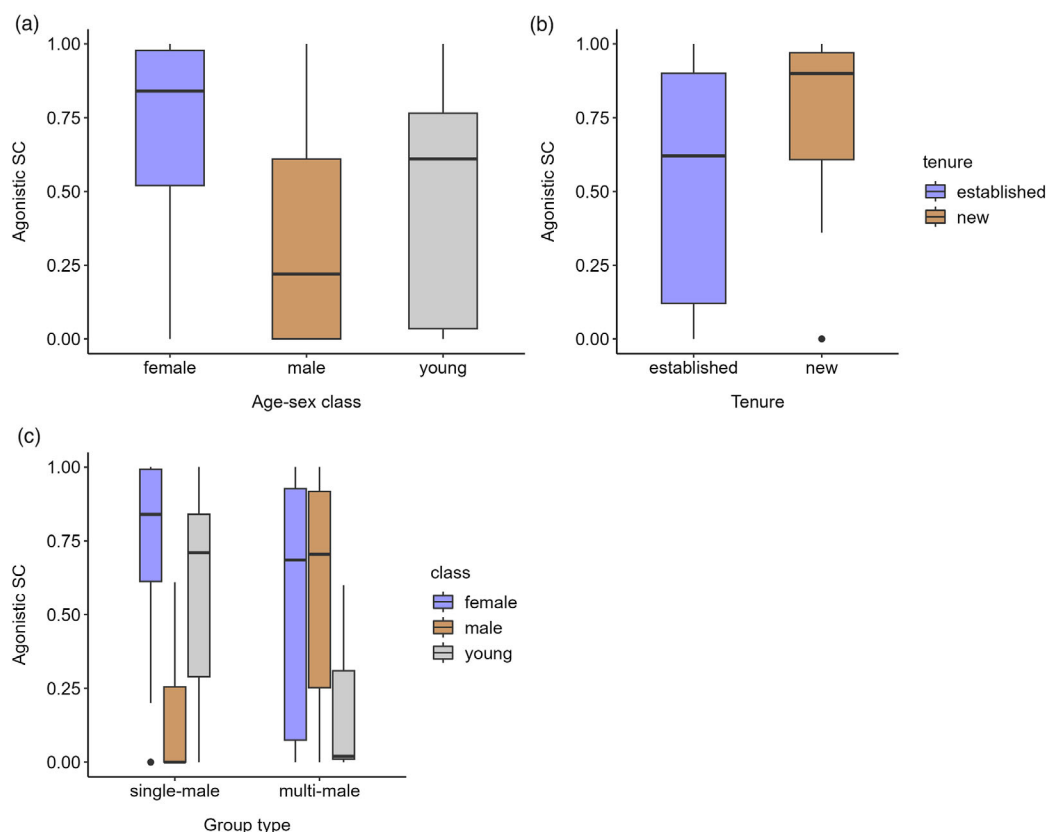
**Figure 4** Relationship between (a) age-sex class (female, male and young), (b) rank DS (David's score) and (c) group type (single- and multi-male) on strength centrality (SC) in proximity networks. The shaded band represents the pointwise 95% confidence interval on the fitted value.



**Figure 5** Relationship between (a) age-sex class (female, male, young), and (b) tenure (established or new member in the group) on strength centrality (SC) in grooming networks.

positive relationship was found between grooming and agonistic behaviours when controlling for genetic relatedness. Therefore, our results do not support that horses possess reconciliatory mechanisms (Shimada & Suzuki, 2020, but see: Cozzi *et al.*, 2010).

Despite the clear relationship reported among the three social networks, their centrality appears to be shaped differently by sociodemographic factors. Higher-ranking individuals had higher values of SC in spatial networks, corroborating several studies on other species (e.g. primates: Janson, 1990;



**Figure 6** Relationship between (a) age-sex class (female, male, young), and (b) tenure (established or new member in the group) by age-class and (c) group type (single-male and multi-male) by age-class on strength centrality (SC) in agonistic networks.

**Table 3** Summary of statistics for a generalized linear mixed model (GLMM) investigating the effect of tenure, rank, strength centrality (SC) of proximity and agonistic social networks on female feral horses' (*Equus ferus caballus*) foaling success in Serra d'Arga, Portugal ( $n = 22$ )

Response variable	Fixed effects	Estimate	SE	<i>t</i>	<i>P</i>	<i>P</i> (perm)
Foaling success (0/1)	(Intercept)	-2.91	1.63	-1.79	0.92	0.16
	SC proximity	2.26	1.32	1.72	0.11	0.22
	SC agonistic	-0.68	1.30	-0.52	0.65	0.69
	<b>Tenure (stable)</b>	<b>2.82</b>	<b>1.16</b>	<b>2.44</b>	<b>0.02</b>	<b>0.03</b>
	Rank DS	-0.76	1.26	-0.60	0.76	0.48

The GLMM controls for female ID. Significance is set at  $P < 0.05$ , and significant fixed effects are highlighted in bold; *P*(perm) is calculated based on permutations ( $n = 10\,000$ ).

Robinson, 1981; van Schaik & van Noordwijk, 1986, spiders: Rayor & Uetz, 1990, birds: Clifton, 1991; Flynn & Giraldeau, 2001, fishes: Krause, 1994). Our findings suggest that being central in the proximity network does not come at a significant cost with respect to access to food for horses, as they are mainly grazers and engage mostly in scramble competition, where food resources are equally available to all individuals (Fleurbaey *et al.*, 2022; Rubenstein & Nuñez, 2009). However, higher centrality may decrease vulnerability to predation (Berger, 1983; Garrott, 1991) which high-ranking individuals seem to be competing for—supporting the selfish herd hypothesis. Moreover, this trade-off may be yet sex-dependent:

being central comes at a reproductive cost for males that must defend their harem against outgroup competitors and predators (Berger, 1986; Feh, 1999; Inoue *et al.*, 2018; Linklater *et al.*, 1999; Pinto *et al.*, 2022), hence males being more peripheral than females on average. Younger females were also more likely to occupy a central position together with adult females and, as a result, they may benefit from associating with higher-ranking females by gaining agonistic support, and eventually engaging in affiliative behaviours (Borgeaud & Bshary, 2015; Mendonça *et al.*, 2021; Schino, 2007; Seyfarth, 1977). Our results revealed a difference in grooming patterns according to age-class, with younger individuals being

more central in grooming networks, corroborating previous studies (primates: Canteloup *et al.*, 2021, horses: Sigurjónsdóttir *et al.*, 2003; Sigurjónsdóttir & Haraldsson, 2019; van Dierendonck *et al.*, 2004). A higher centrality in affiliative networks may confer more protection to young individuals against intra- and inter-group competition and be used as a strategy to avoid receiving aggression. This is supported by the results on agonistic networks, revealing that young individuals did not engage in agonistic behaviours more often than adult females (but see: Sigurjónsdóttir & Haraldsson, 2019). In matrilineal societies, where young females do not disperse from their natal group, the formation and maintenance of social bonds may result in long-term and long-lasting benefits for young females (Silk, 2003; Silk *et al.*, 2007). However, in societies with female natal dispersal, such as in horses, allocating time and energy to bond before dispersal may seem counter-productive. Previous studies have reported that females tend to disperse to groups with familiar females; therefore, forging strong social bonds with females from the same natal group may facilitate integration into new harems later on (Monard & Duncan, 1996). Moreover, engaging in affiliative behaviours allows young females to develop their social skills, which might be beneficial in bond formation when integrating into a new harem (Cameron *et al.*, 2009). In contrast, old and well-established horses may have already formed social bonds, therefore their need to actively engage in grooming may be reduced (Sigurjónsdóttir & Haraldsson, 2019).

Overall, females dominated agonistic networks. While inter-group aggression is led mostly by males fending for their harem females (Feh, 1999; Pinto *et al.*, 2022; Rubenstein, 1982), intra-group competition is predominantly females' territory, as they compete for access to food resources. Agonism seems to increase in newly integrated females, as they go through the process of integration and a new group hierarchy is being established (Granquist *et al.*, 2012; Nuñez *et al.*, 2014, but see Rutberg & Greenberg, 1990). Better-established females were more likely to foal in the following BS than recently transferred females, corroborating that female integration can be costly for females and hence result in a lower reproductive success (Nuñez *et al.*, 2014).

Additionally, our results revealed higher levels of agonism and lower proximity among individuals in single-male groups, suggesting an increased female–female competition in groups with a single male. This agrees with previous studies showing that the presence of adult males is linked to decreased agonistic interactions (Berger, 1977; Sigurjónsdóttir & Haraldsson, 2019). Although female centrality is lower in agonistic networks in multi-male groups, male centrality increases, likely as a result of increased intra-group male–male competition. Therefore, we suggest that the presence of a second male may act as a buffer for male-to-female aggression. A possible adaptive explanation for the existence of multiple-male groups may rely on the fact that it reduces female–female competition, which could ultimately lead to an increased female reproductive success.

To conclude, our study is the first to examine the interconnectedness among three different social networks, controlling

for genetic relatedness at a population level in equids. Furthermore, we investigated the influence of sociodemographic factors on the centrality of three different social networks, discussing the costs and benefits associated with social network positioning and the potential implications for individuals' fitness in non-matrilineal societies. Overall, our results provide a step forward in understanding the mechanisms leading to social cohesion, and the ultimate benefits of sociality in non-matrilineal species, namely in populations under a constant threat from predation and human pressures.

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## Author contributions

RM designed the study. RM and PP collected behavioural data. RM, TM and SI contributed to data analyses. RM wrote the first draft of the manuscript. All authors contributed to the final version of the manuscript.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

### Appendix S1. Supplementary material.

**Figure S1.** Kernel density plot showing observed and random distributions for dyadic inter-individual distance. Inter-individual distance is not random given that the permuted

inter-individual and observed inter-individual distance differed significantly according to Wilcoxon test for dependent samples ( $V = 22\ 131\ 965$ ,  $P < 0.001$ ).

**Table S1.** Information on group characteristics, individuals' sex-age class, standardized David's Score ( $DS_i'$ ) ranging from 0 to 1 (0 corresponding to the most subordinate and 1 to the most dominant individual) and network attributes (strength centrality – SC and normalized strength centrality –  $SC'$ ) of proximity, grooming and agonistic networks.

**Table S2.** Summary of statistics for four separate generalized linear mixed models (GLMMs) investigating the effects of distance DI on proximity SRI, proximity SRI on grooming SRI and Agonistic SRI, as well as the effect of agonistic SRI on grooming SRI.

**Table S3.** Summary of statistics for four separate generalized linear mixed models (GLMMs) investigating the effects of distance DI on proximity SRI, proximity SRI on grooming SRI and Agonistic SRI, as well as the effect of agonistic SRI on grooming SRI.

**Table S4.** Summary of statistics for three separate generalized linear mixed models (GLMMs) investigating the effects of age-sex class, tenure, rank and group type on strength centrality (SC) of proximity, grooming and agonistic social networks of feral horses (*Equus ferus caballus*) in Serra d'Arga, Portugal.

**Table S5.** Summary of statistics for a generalized linear mixed model (GLMM) investigating the effect of tenure, rank, strength centrality (SC) of proximity and agonistic social networks on female feral horses' (*Equus ferus caballus*) foaling success in Serra d'Arga, Portugal ( $n = 22$ ).