

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

R. S. Mendonça^{1,2}

T. Maeda^{1,3}

P. Pinto¹

S. Inoue^{1,4}

M. Ringhofer⁵

S. Yamamoto⁶

S. Hirata¹

1. Wildlife Research Center, Kyoto University, Kyoto, Japan

2. Centre for Functional Ecology – Science for People & the Planet, Department of Life Sciences, University of Coimbra, Coimbra, Portugal

3. School of Advanced Sciences, The Graduate University for Advanced Studies (SOKENDAI), Kanagawa, Japan

4. Graduate School of Environmental Science, Nagoya University, Nagoya, Japan

5. Department of Animal Sciences, Teikyo University of Science, Yamanashi, Japan

6. Institute for Advanced Study, Kyoto University, Kyoto, Japan

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 (Blaszczyk, [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), totalling 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:

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

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:

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

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:

$$SC' = \frac{SC_i - SC_{\max}}{SC_{\max} - SC_{\min}}$$

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.

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: $t = 2.62$, $P = 0.01$).

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 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; 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 (Fleurance 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.

Acknowledgements

We thank Viana do Castelo City, Montaria Village and Tetsuro Matsuzawa for supporting our project. We also are grateful to the volunteers who contributed to data collection. This study was financially supported by JSPS Core-to-Core CCSN, JSPS-LGPU04, JSPS KAKENHI (18H05524 to SH, 17H05862 and 19H00629 to SY, 18K18342 to MR) and Kyoto University SPIRITS to SH. We thank Clio Reid, PhD, from Edanz (<https://jp.edanz.com/ac>) for editing a draft of this manuscript.

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	<i>N</i> males	<i>N</i> females	Young individuals ^a	Hours observed ^b	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

Breeding season	Group name	Group size	<i>N</i> males	<i>N</i> females	Young individuals ^a	Hours observed ^b	Total of drone scans
	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

Breeding season	Group name	Group size	<i>N</i> males	<i>N</i> females	Young	Hours observed ^a	Total of drone scans
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.

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

^b 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.

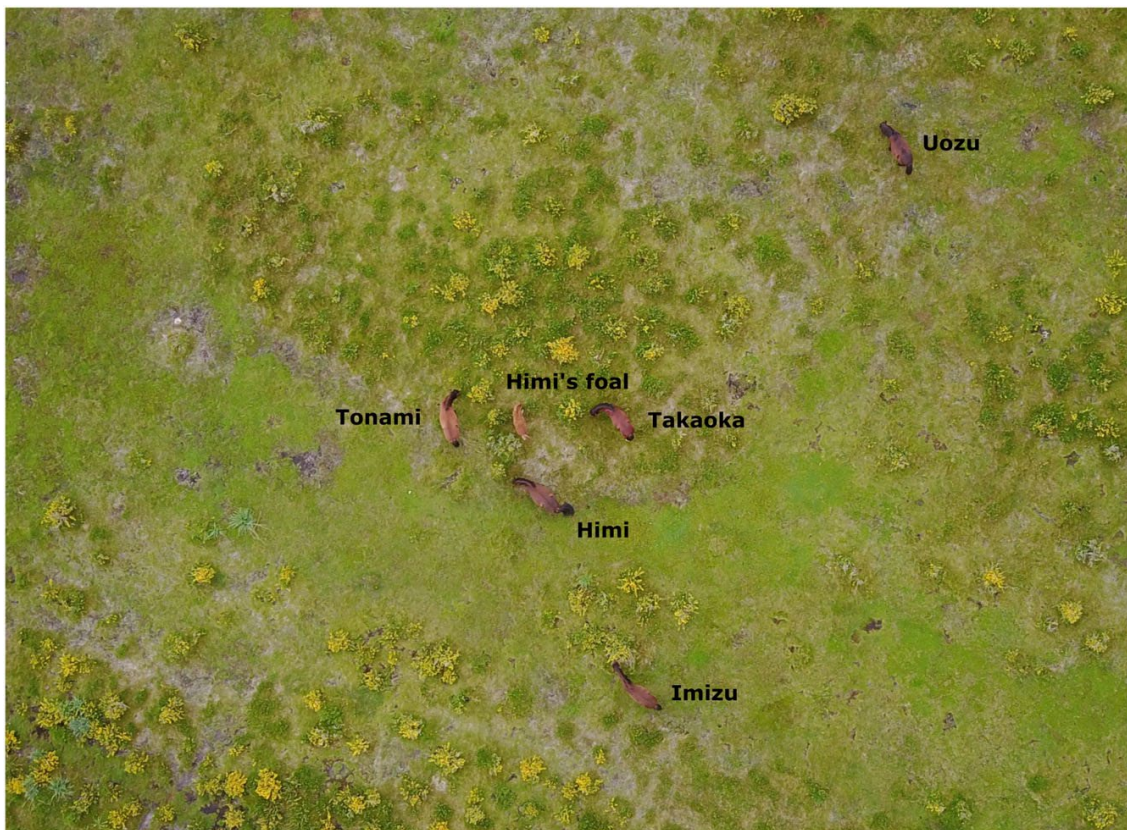


Figure 1

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

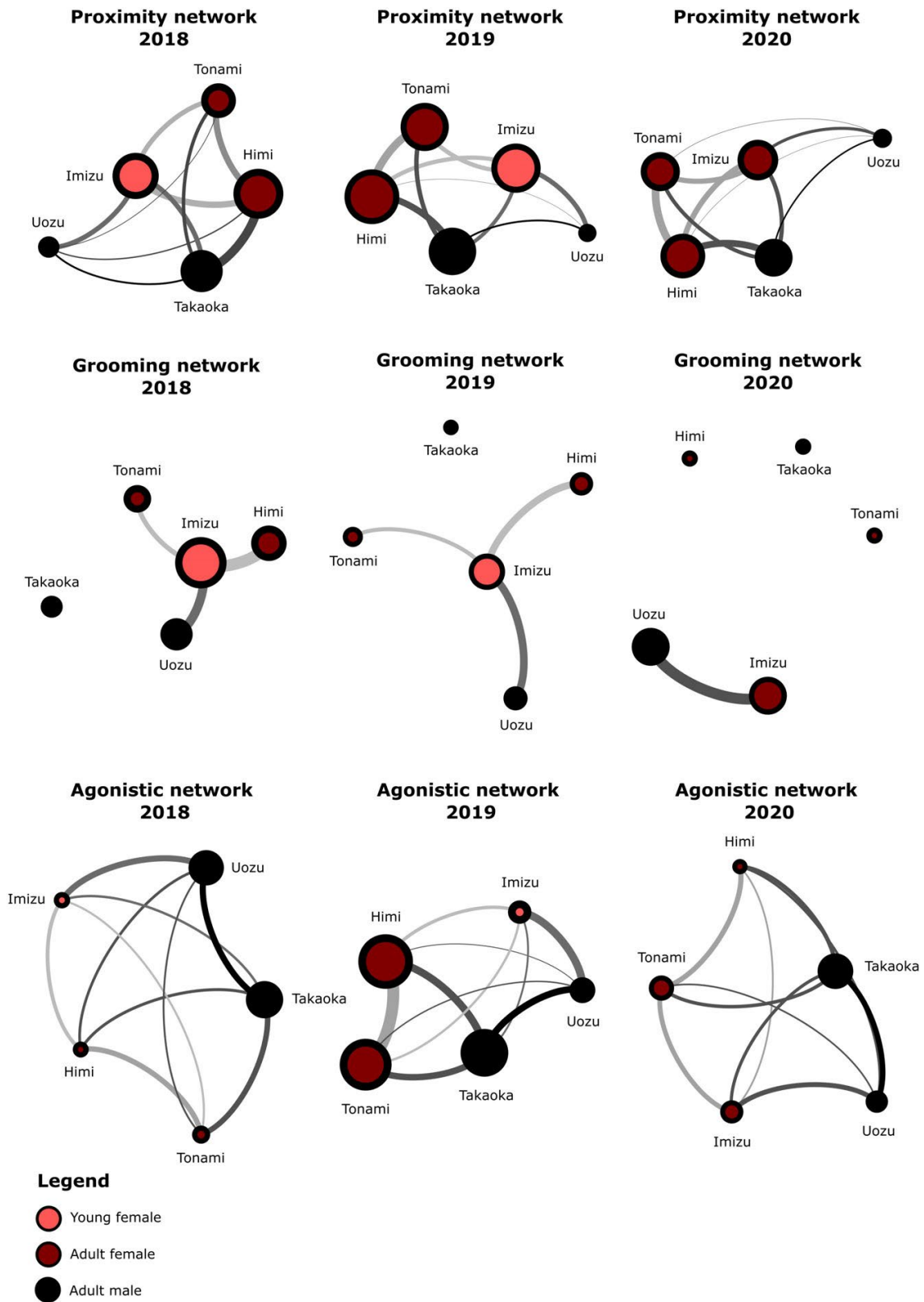


Figure 2

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.

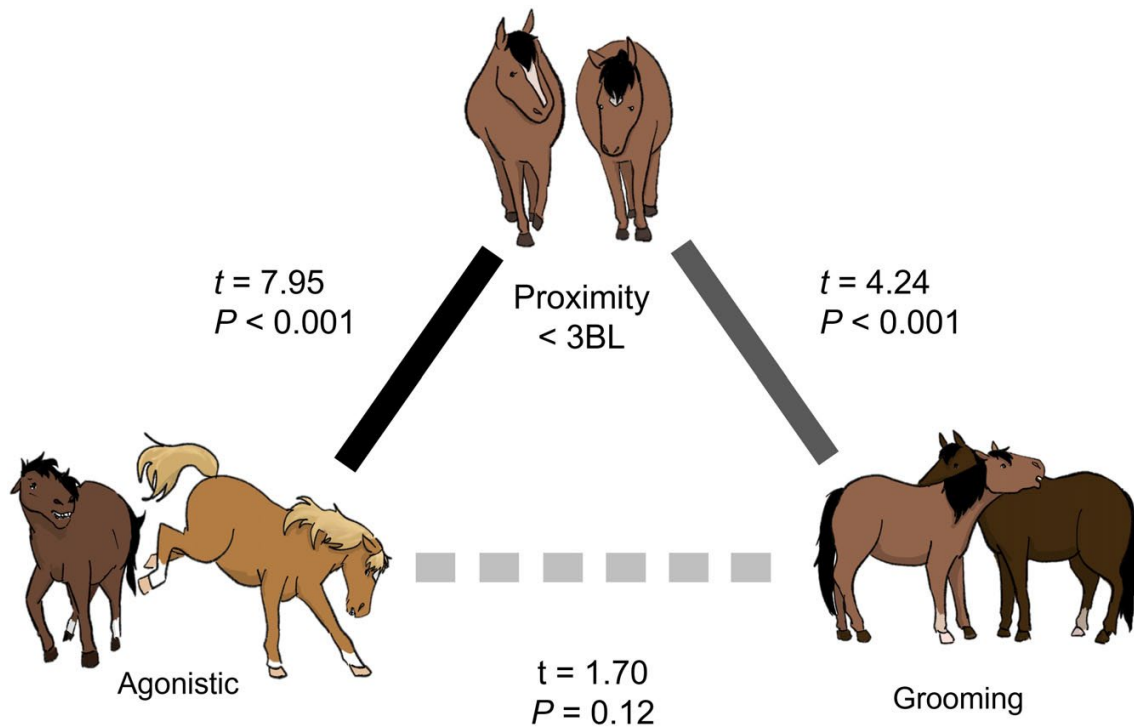


Figure 3

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 $P < 0.05$.

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
	Class (male)	-0.56	0.07	-8.04	< 0.001
	Class (young)	0.09	0.09	0.99	0.25
	Tenure (established)	0.05	0.06	0.90	0.50
	Rank DS	0.36	0.08	4.31	< 0.001
	Group type (multi-male)	0.23	0.06	3.72	< 0.001
SC grooming network	(Intercept)	0.27	0.09	2.86	0.00
	Class (male)	0.08	0.09	0.91	0.36
	Class (young)	0.27	0.11	2.45	0.01
	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
	(Intercept)	0.87	0.08	10.73	0.00

Response variables	Fixed effects	Estimate	SE	<i>t</i>	<i>P</i>
	Class (male)	-0.56	0.09	-6.06	< 0.001
	Class (young)	-0.17	0.11	-1.55	0.15
	Tenure (established)	-0.21	0.07	-3.20	0.02
SC agonistic network	Rank DS	-0.01	0.09	-0.10	1.00
	Group type (multi-male)	-0.14	0.09	-1.55	0.05
	Group type (multi-male): Class (male)	0.60	0.15	4.06	< 0.001
	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 ($n = 10\ 000$).

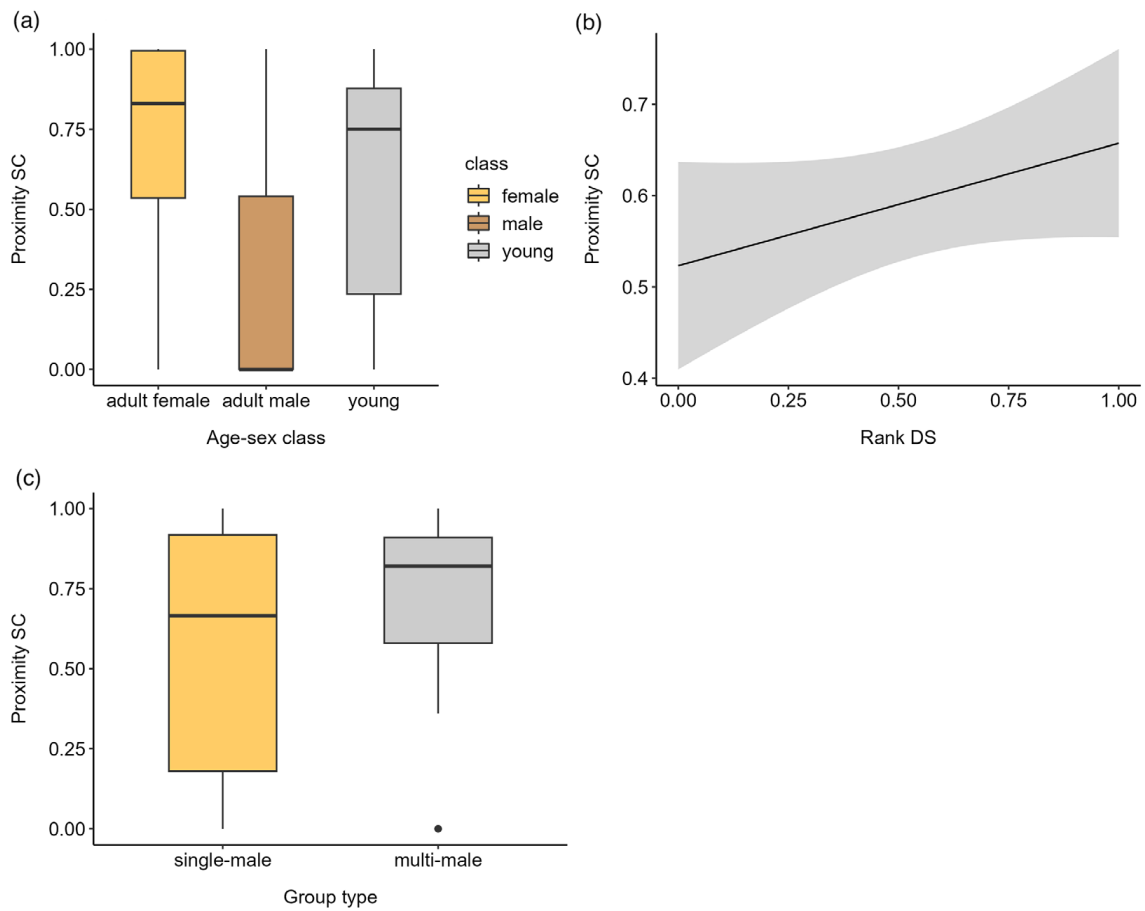


Figure 4

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.

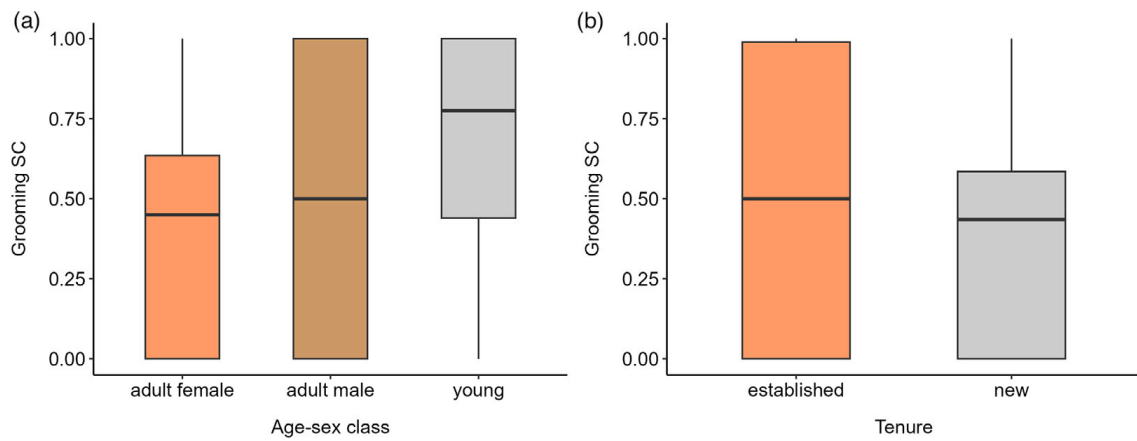


Figure 5

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.

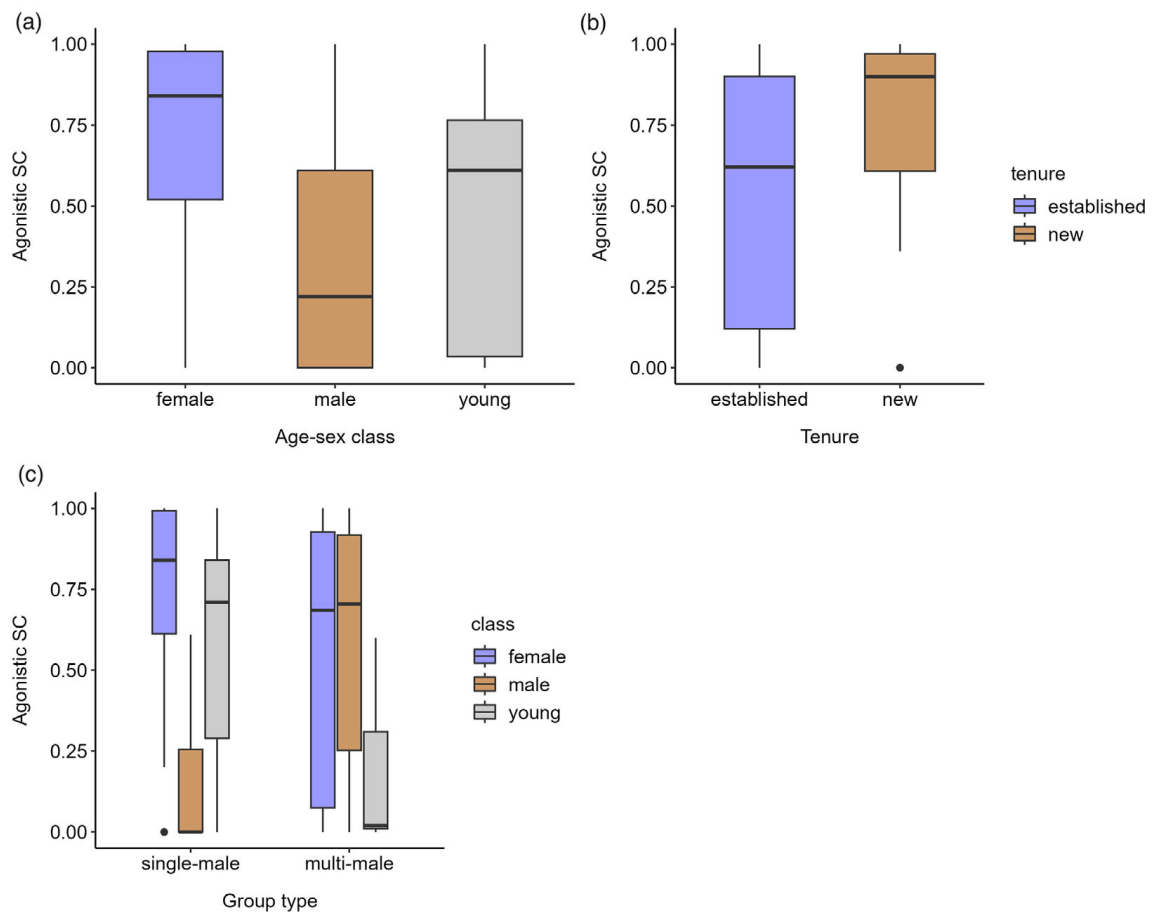


Figure 6

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	t	P	$P(\text{perm})$
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

Response variable	Fixed effects	Estimate	SE	<i>t</i>	<i>P</i>	<i>P</i> (perm)
	SC agonistic	-0.68	1.30	-0.52	0.65	0.69
	Tenure (stable)	2.82	1.16	2.44	0.02	0.03
	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; $P(\text{perm})$ is calculated based on permutations ($n = 10\,000$).

References

- Archie, E. A., Morrison, T. A., Foley, C. A. H., Moss, C. J., & Alberts, S. C. (2006). Dominance rank relationships among wild female African elephants (*Loxodonta africana*). *Animal Behaviour*, 71(1), 117–127.
- Arseneau-Robar, T. J. M., Joyce, M. M., Stead, S. M., & Teichroeb, J. A. (2018). Proximity and grooming patterns reveal opposite-sex bonding in Rwenzori Angolan colobus monkeys (*Colobus angolensis ruwenzorii*). *Primates*, 59(3), 267–279.
- Ashton, B. J., Thornton, A., & Ridley, A. R. (2019). Larger group sizes facilitate the emergence and spread of innovations in a group-living bird. *Animal Behaviour*, 158, 1–7.
- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266(1420), 665–670.
- Berger, J. (1977). Organizational systems and dominance in feral horses in the grand canyon. *Behavioral Ecology and Sociobiology*, 2, 131–146.
- Berger, J. (1983). Induced abortion and social factors in wild horses. *Nature*, 303, 59–61.
- Berger, J. (1986). *Wild horses of the great basin*. University of Chicago Press.
- Blaszczyk, M. B. (2018). Consistency in social network position over changing environments in a seasonally breeding primate. *Behavioral Ecology and Sociobiology*, 72(1), 1–13.
- Borgeaud, C., & Bshary, R. (2015). Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in experimentally induced conflicts. *Current Biology*, 25(22), 3011–3016.

- Borgeaud, C., Sosa, S., Sueur, C., & Bshary, R. (2017). The influence of demographic variation on social network stability in wild vervet monkeys. *Animal Behaviour*, 134, 155–165.
- Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, 35(5), 1454–1469.
- Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *PNAS*, 106, 13850–13853.
- Canteloup, C., Puga-Gonzalez, I., Sueur, C., & van de Waal, E. (2021). The consistency of individual centrality across time and networks in wild vervet monkeys. *American Journal of Primatology*, 83(2), e23232.
- Christensen, J. W., Zharkikh, T., Ladewig, J., & Yasinetskaya, N. (2002). Social behaviour in stallion groups (*Equus przewalskii*) and (*Equus caballus*) kept under natural and domestic conditions. *Applied Animal Behaviour Science*, 76(1), 11–20.
- Clifton, K. E. (1991). Subordinate group members act as food- finders within striped parrotfish territories. *Journal of Experimental Marine Biology and Ecology*, 145(2), 141–148.
- Cozzi, A., Sighieri, C., Gazzano, A., Nicol, C. J., & Baragli, P. (2010). Post-conflict friendly Reunion in a permanent group of horses (*Equus caballus*). *Behavioural Processes*, 85(2), 185–190.
- Crofoot, M. C., Rubenstein, D. I., Maiya, A. S., & Berger-Wolf, T. Y. (2011). Aggression, grooming and group-level cooperation in white-faced capuchins (*Cebus capucinus*): Insights from social networks. *American Journal of Primatology*, 73(8), 821–833.
- Croft, D. P., Madden, J. R., Franks, D. W., & James, R. (2011). Hypothesis testing in animal social networks. *Trends in Ecology & Evolution*, 26(10), 502–507.
- David, H. A. (1987). Ranking from unbalanced paired- comparison data. *Biometrika*, 74, 432–436.
- de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, 71, 585–592.
- Dunbar, R. I. (1991). Functional significance of social grooming in primates. *Folia Primatologica*, 57(3), 121–131.
- Duncan, P. (1992). *Horses and grasses: The nutritional ecology of equids and their impact on the Camargue*. Springer-Verlag.
- Farine, D. R., & Sheldon, B. C. (2015). Selection for territory acquisition is modulated by social network structure in a wild songbird. *Journal of Evolutionary Biology*, 28(3), 547–556.
- Feh, C. (1988). Social behavior and relationships of Przewalski horses in Dutch semi-reserves. *Applied Animal Behaviour Science*, 21(1–2), 71–87.

- Feh, C. (1999). Alliances and reproductive success in Camargue stallions. *Animal Behaviour*, 57, 705–713.
- Fleurance, G., Rossignol, N., & Dumont, B. (2022). Diurnal observations of feeding choices in grazing horses correctly predict their daily diet composition. *Applied Animal Behaviour Science*, 252, 105652.
- Flynn, R. E., & Giraldeau, L. A. (2001). Producer–scrounger games in a spatially explicit world: Tactic use influences flock geometry of spice finches. *Ethology*, 107(3), 249–257.
- Formica, V. A., Wood, C. W., Larsen, W. B., Butterfield, R. E., Augat, M. E., Hougen, H. Y., & Brodie Iii, E. D. (2012). Fitness consequences of social network position in a wild population of forked fungus beetles (*Bolitotherus cornutus*). *Journal of Evolutionary Biology*, 25(1), 130–137.
- Galef, B. G., & Giraldeau, L. A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour*, 61(1), 3–15.
- Garrott, R. A. (1991). Sex ratios and differential survival of feral horses. *The Journal of Animal Ecology*, 60, 929–936.
- Go, C. K., Ringhofer, M., Lao, B., Kubo, T., Yamamoto, S., & Ikeda, K. (2020). A mathematical model of herding in horse- harem group. *Journal of Ethology*, 38(3), 343–353.
- Granquist, S. M., Thorhallsdottir, A. G., & Sigurjonsdottir, H. (2012). The effect of stallions on social interactions in domestic and semi feral harems. *Applied Animal Behaviour Science*, 141(1–2), 49–56.
- Hall, C. L., & Fedigan, L. M. (1997). Spatial benefits afforded by high rank in white-faced capuchins. *Animal Behaviour*, 53 (5), 1069–1082.
- Hamede, R. K., Bashford, J., McCallum, H., & Jones, M. (2009). Contact networks in a wild Tasmanian devil (*Sarcophilus harrisii*) population: Using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecology Letters*, 12(11), 1147–1157.
- Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31(2), 295–311.
- Heitor, F., do Mar Oom, M., & Vicente, L. (2006). Social relationships in a herd of Sorraia horses: Part I. correlates of social dominance and contexts of aggression. *Behavioural Processes*, 73(2), 170–177.
- Hex, S. B., Tombak, K., & Rubenstein, D. I. (2021). A new classification of mammalian uni-male multi-female groups based on the fundamental principles governing inter-and intrasexual relationships. *Behavioral Ecology and Sociobiology*, 75(11), 157.
- Hirsch, B. T. (2007). Costs and benefits of within-group spatial position: A feeding competition model. *The Quarterly Review of Biology*, 82(1), 9–27.

- Hoppitt, W. J., & Farine, D. R. (2018). Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Animal Behaviour*, 136, 227–238.
- Inoue, S., Yamamoto, S., Ringhofer, M., Mendonça, R. S., & Hirata, S. (2020). Lateral position preference in grazing feral horses. *Ethology*, 126(1), 111–119.
- Inoue, S., Yamamoto, S., Ringhofer, M., Mendonça, R. S., Pereira, C., & Hirata, S. (2018). Spatial positioning of individuals in a group of feral horses, a case study using drone technology. *Mammal Research*, 64, 249–259.
- Inoue, S., Yamamoto, S., Ringhofer, M., Mendonça, R. S., Pereira, C., & Hirata, S. (2019). Spatial positioning of individuals in a group of feral horses: A case study using drone technology. *Mammal Research*, 64(2), 249–259.
- Janson, C. H. (1990). Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, 40(5), 922–934.
- Janson, C. H., & van Schaik, C. P. (1993). Ecological risk aversion in juvenile primates: Slow and steady wins the race. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates: Life history, development and behaviour* (pp. 57–74). Oxford University Press.
- Krause, J. (1994). The influence of food competition and predation risk on size-assortative shoaling in juvenile chub (*Leuciscus cephalus*). *Ethology*, 96(2), 105–116.
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.
- Krebs, J. R., & Davies, N. B. (2009). *Behavioural ecology: An evolutionary approach*. John Wiley & Sons.
- Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behavior*, 74(6), 1617–1629.
- Linklater, W. L., Cameron, E. Z., Minot, E. O., & Stafford, K. J. (1999). Stallion harassment and the mating system of horses. *Animal Behaviour*, 58(2), 295–306.
- Loehle, C. (1995). Social barriers to pathogen transmission in wild animal populations. *Ecology*, 76(2), 326–335.
- MacIntosh, A. J., Jacobs, A., Garcia, C., Shimizu, K., Mouri, K., Huffman, M. A., & Hernandez, A. D. (2012). Monkeys in the middle: Parasite transmission through the social network of a wild primate. *PLoS One*, 7(12), e51144.
- Maeda, T., Ochi, S., Ringhofer, M., Sosa, S., Sueur, C., Hirata, S., & Yamamoto, S. (2021). Aerial drone observations identified a multilevel society in feral horses. *Scientific Reports*, 11(1), 1–12.
- Maeda, T., Sueur, C., Hirata, S., & Yamamoto, S. (2021). Behavioural synchronization in a multilevel society of feral horses. *PLoS One*, 16(10), e0258944.

- McDonald, D. B. (2007). Predicting fate from early connectivity in a social network. *PNAS*, 104(26), 10910–10914.
- McDonnell, M. D. (2003). *The equid ethogram, a practical field guide to horse behavior*. The Blood–Horse.
- Mendonça, R. S., Pinto, P., Inoue, S., Ringhofer, M., Godinho, R., & Hirata, S. (2021). Social determinants of affiliation and cohesion in a population of feral horses. *Applied Animal Behaviour Science*, 245, 105496.
- Mendonça, R. S., Pinto, P., Maeda, T., Inoue, S., Ringhofer, M., Yamamoto, S., & Hirata, S. (2022). Population characteristics of feral horses impacted by anthropogenic factors and their management implications. *Frontiers in Ecology and Evolution*, 10, 848741.
- Mendonça, R. S., Ringhofer, M., Pinto, P., Inoue, S., & Hirata, S. (2020). Feral horses' (*Equus ferus caballus*) behavior toward dying and dead conspecifics. *Primates*, 61(1), 49–54.
- Monard, A., & Duncan, P. (1996). Consequences of natal dispersal in female horses. *Animal Behaviour*, 52, 565–579.
- Nakamura, M., Rio-Maior, H., Godinho, R., Petrucci-Fonseca, F., & Álvares, F. (2021). Source-sink dynamics promote wolf persistence in human-modified landscapes: Insights from long-term monitoring. *Biological Conservation*, 256, 109075.
- Nunñez, C. M., Adelman, J. S., & Rubenstein, D. I. (2015). Sociality increases juvenile survival after a catastrophic event in the feral horse (*Equus caballus*). *Behavioral Ecology*, 26(1), 138–147.
- Nunñez, C. M., Adelman, J. S., Smith, J., Gesquiere, L. R., & Rubenstein, D. I. (2014). Linking social environment and stress physiology in feral mares (*Equus caballus*): Group transfers elevate fecal cortisol levels. *General and Comparative Endocrinology*, 196, 26–33.
- Oh, K. P., & Badyaev, A. V. (2010). Structure of social networks in a passerine bird: Consequences for sexual selection and the evolution of mating strategies. *The American Naturalist*, 176(3), E80–E89.
- Pinto, P., & Hirata, S. (2020). Does size matter? Examining the possible mechanisms of multi-stallion groups in horse societies. *Behavioural Processes*, 181, 104277.
- Pinto, P., Mendonça, R. S., & Hirata, S. (2022). Examining the costs and benefits of male-male associations in a group-living equid. *Applied Animal Behaviour Science*, 253, 105660.
- Rasa, O. A. E. (1989). The costs and effectiveness of vigilance behaviour in the dwarf mongoose: Implications for fitness and optimal group size. *Ethology Ecology and Evolution*, 1(3), 265–282.

- Rayor, L. S., & Uetz, G. W. (1990). Trade-offs in foraging success and predation risk with spatial position in colonial spiders. *Behavioral Ecology and Sociobiology*, 27(2), 77–85.
- Rhine, R. J., Forthman, D. L., Stillwell-Barnes, R., Westlund, B. J., & Westlund, H. D. (1981). Movement patterns of yellow baboons (*Papio cynocephalus*): Sex differences in juvenile development toward adult patterns. *American Journal of Physical Anthropology*, 55(4), 473–484.
- Ringhofer, M., Go, C. K., Inoue, S., Mendonça, R. S., Hirata, S., Kubo, T., & Yamamoto, S. (2020). Herding mechanisms to maintain the cohesion of a harem group: Two interaction phases during herding. *Journal of Ethology*, 38(1), 71–77.
- Ringhofer, M., Inoue, S., Mendonça, R. S., Pereira, C., Matsuzawa, T., Hirata, S., & Yamamoto, S. (2017). Comparison of the social systems of primates and feral horses: Data from a newly established horse research site on Serra D'Arga, northern Portugal. *Primates*, 58(4), 479–484.
- Roberts, J. M., & Browning, B. A. (1998). Proximity and threats in highland ponies. *Social Networks*, 20(3), 227–238.
- Robinson, J. G. (1981). Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. *Animal Behaviour*, 29(4), 1036–1056.
- Ron, T., Henzi, S. P., & Motro, U. (1996). Do female chacma baboons compete for a safe spatial position in a southern woodland habitat? *Behaviour*, 133(5–6), 475–490.
- Rubenstein, D. I. (1978). On predation, competition, and the advantages of group living. *Perspectives in Ethology*, 3, 205–231.
- Rubenstein, D. I. (1982). Risk, uncertainty and evolutionary strategies. In King's College Sociobiol. Group (Ed.), *Current Problems in Sociobiology* (pp. 91–111). Cambridge University Press.
- Rubenstein, D. I. (1994). The ecology of female social behaviour in horses, zebras and asses. In P. J. Jarman & A. Rossiter (Eds.), *Animal societies: Individuals, interactions, and organization* (pp. 13–28). Kyoto University Press.
- Rubenstein, D. I., & Núñez, C. M. (2009). Sociality and reproductive skew in horses and zebras. In R. Hager & C. B. Jones (Eds.), *Reproductive skew in vertebrates: Proximate and ultimate causes* (pp. 196–226). Cambridge University Press.
- Rutberg, A. T., & Greenberg, S. A. (1990). Dominance, aggression frequencies and modes of aggressive competition in feral pony mares. *Animal Behaviour*, 40(2), 322–331.
- Schino, G. (2007). Grooming and agonistic support: A meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, 18 (1), 115–120.

- Schino, G., & Alessandrini, A. (2015). Short-term costs and benefits of grooming in Japanese macaques. *Primates*, 56(3), 253–257.
- Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65(4), 671–698.
- Seyfarth, R. M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour*, 28(3), 798–813.
- Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, 308(5959), 541–543.
- Shimada, M., & Sueur, C. (2018). Social play among juvenile wild Japanese macaques (*Macaca fuscata*) strengthens their social bonds. *American Journal of Primatology*, 80(1), e22728.
- Shimada, M., & Suzuki, N. (2020). The contribution of mutual grooming to affiliative relationships in a feral Misaki horse herd. *Animals*, 10(9), 1564.
- Sigurjo'nsdo'ttir, H., & Haraldsson, H. (2019). Significance of group composition for the welfare of pastured horses. *Animals*, 9(1), 14.
- Sigurjo'nsdo'ttir, H., Snorrason, S., van Dierendonck, M., & Tho'rhallsdo'ttir, A. (2003). Social relationships in a group of horses without a mature stallion. *Behaviour*, 140(6), 783–804.
- Silk, J. B. (2007). Social components of fitness in primate groups. *Science*, 317(5843), 1347–1351.
- Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, 61(2), 183–195.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, 20 (15), 1359–1361.
- Smith, J. E., Memenis, S. K., & Holekamp, K. E. (2007). Rank-related partner choice in the fission-fusion society of the spotted hyena (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology*, 61, 753–765.
- Smith, V. A., King, A. P., & West, M. J. (2002). The context of social learning: Association patterns in a captive flock of brown-headed cowbirds. *Animal Behaviour*, 63(1), 23–35.
- Snyder-Mackler, N., Burger, J. R., Gaydosh, L., Belsky, D. W., Noppert, G. A., Campos, F. A., Bartolomucci, A., Yang, Y. C., Aiello, A. E., O'Rand, A., & Harris, K. M. (2020). Social determinants of health and survival in humans and other animals. *Science*, 368(6493), eaax9553.
- Sosa, S. (2016). The influence of gender, age, matriline and hierarchical rank on individual social position, role and interactional patterns in *Macaca sylvanus* at

- 'La Forêt des singes': A multilevel social network approach. *Frontiers in Psychology*, 7, 529.
- Sosa, S., Jacoby, D. M., Lihoreau, M., & Sueur, C. (2021). Animal social networks: Towards an integrative framework embedding social interactions, space and time. *Methods in Ecology and Evolution*, 12(1), 4–9.
- Sosa, S., Puga-Gonzalez, I., Hu, F., Pansanel, J., Xie, X., & Sueur, C. (2020). A multilevel statistical toolkit to study animal social networks: The animal network toolkit software (ANTs) R package. *Scientific Reports*, 10(1), 1–8.
- Stanley, C. R., Mettke-Hofmann, C., Hager, R., & Shultz, S. (2018). Social stability in semiferal ponies: Networks show interannual stability alongside seasonal flexibility. *Animal Behaviour*, 136, 175–184.
- Sterck, E. H., Watts, D. P., & Van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41(5), 291–309.
- Tong, W., Shapiro, B., & Rubenstein, D. I. (2015). Genetic relatedness in two-tiered plains zebra societies suggests that females choose to associate with kin. *Behaviour*, 152(15), 2059–2078.
- Turner, J. W., Bills, P. S., & Holekamp, K. E. (2018). Ontogenetic change in determinants of social network position in the spotted hyena. *Behavioral Ecology and Sociobiology*, 72(1), 1–15.
- van Dierendonck, M. C., Sigurjónsdóttir, H., Colenbrander, B., & Thorhallsdóttir, A. G. (2004). Differences in social behaviour between late pregnant, post-partum and barren mares in a herd of Icelandic horses. *Applied Animal Behaviour Science*, 89(3–4), 283–297.
- van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Stand & R. Foley (Eds.), *Comparative Socioecology: The behavioral ecology of humans and other mammals* (pp. 195–218). Blackwell.
- van Schaik, C. P., & Janson, C. H. (1988). Recognizing the many faces of primate food competition: Methods. *Behaviour*, 105(1–2), 165–186.
- van Schaik, C. P., & van Noordwijk, M. A. (1986). The hidden costs of sociality: Intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). *Behaviour*, 99(3–4), 296–314.
- Vehrencamp, S. L. (1983). A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, 31(3), 667–682.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75(3–4), 262–300.
- Wiszniewski, J., Lusseau, D., & Möller, L. M. (2010). Female bisexual kinship ties maintain social cohesion in a dolphin network. *Animal Behaviour*, 80(5), 895–904.

Wooddell, L. J., Kaburu, S. S., & Dettmer, A. M. (2019). Dominance rank predicts social network position across developmental stages in rhesus monkeys. *American Journal of Primatology*, 82(11), e23024.

Wooddell, L. J., Kaburu, S. K., & Dettmer, A. M. (2020). Dominance rank predicts social network position across developmental stages in rhesus monkeys. *American Journal of Primatology*, 82, e23024.

Supporting Information

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^0) 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^0) 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 ($n = 22$).