

Social networks of reintroduced Przewalski's horses in the Great Gobi B Strictly Protected Area (Mongolia)

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Abstract

Analyzing social networks is a powerful tool for understanding the ecology of social species. While most studies focus on the role of each group member, few compare groups with different characteristics. The current population of Przewalski's horses *Equus ferus przewalskii* at the Great Gobi B Strictly Protected Area (Mongolia) includes groups of wild-born and captive-bred individuals with different experiences with the area (acclimatizing, long-term reintroduced, and wild-born), therefore serving as an ideal natural behavioral lab. We filmed 11 groups for 141.5 hours in summer 2018 (July), late spring 2019 (May, June), and autumn 2019 (September, October). Affiliative and agonistic interactions were recorded, and social networks were created. We tested the influence of origin, experience, season, sex, age, relative time belonging to the group, relatedness, and dominance rank on different network indices at the individual and group levels. We found that groups with greater experience in the area are generally better connected than members of the newly formed groups. However, these strong networks were created by wild-born individuals with very low interaction rates. On the contrary, inexperienced groups composed of captive-bred individuals displayed many interactions but created weak social networks. The results show a trend of behavioral transition from acclimatizing through long-term reintroduced to wild-born groups, supporting that the newly formed groups of released Przewalski's horses need time to display the typical social behavior patterns of wild-born individuals. Long-term monitoring of released Przewalski's horses is recommended to promote the success of this reintroduction program.

Key words: Przewalski's horses, reintroduction, social behavior, soft-release.

Studying the social behavior and networks of large social ungulates is a crucial aspect of understanding their adaptation to the environment, and is vital to their survival (Knight 2001; Conradt et al. 2009; Bousquet 2011; Macdonald 2016; Sniijders et al. 2017). Long-term monitoring assessing the adaptation of the animals to the new conditions (Sarrazin and Barbault 1996; Seddon 1999; Fischer and Lindenmayer 2000) and creating socially functional populations (Goldenberg et al. 2019) is especially important for reintroduced populations (Berger-Tal et al. 2011; IUCN/SSC 2013). The adaptability of animals will be affected by their origin (captive-breeding), reintroduction technique (commonly through soft-release methods), familiarity (Shier 2006; Moseby et al. 2020), and life experiences, which significantly influence social behavior and reintroduction success (Berger-Tal et al. 2011). Animals captured from wild populations (i.e., wild-born individuals) fare better after release than those reared in captivity (Fischer & Lindenmayer 2000; Teixeira et al. 2007; Dickens et al. 2010). Captivity might also promote the development of behavioral characteristics (such as higher aggressiveness or boldness) that may jeopardize their survival (Baker et al. 1998; Bremner-Harrison et al. 2004; Kelley et al. 2006). Personality and social behavior within the group can also

strongly impact reintroduction success (Gusset et al. 2010; Gaudioso et al. 2011).

The Przewalski's horse was listed as Extinct in the wild in 1996 and as Endangered since 2011 thanks to ongoing captive breeding and reintroduction efforts (King et al. 2015). As described by Scheibe et al. (1997) and Pereladova et al. (1999), the behavior of reintroduced Przewalski's horses differs from the typical pattern of wild conspecifics in the first year after release. Just after this period, horses show a similar yearly activity budget to that observed among wild Przewalski's horses. Przewalski's horses live in non-territorial stable family groups (harems) composed of one (or more) adult stallions, several mares, and their offspring (Boyd et al. 2016). Females' and males' priorities are the main determinants of group cohesiveness in horses: females prioritize consistent access to feed, water, and a low risk of intraspecific harassment (Rubenstein 1994; Nowzari et al. 2013; Schoenecker et al. 2016), while males prioritize the proximity to females and a reduced probability of costly conflicts (Berger 1986; Rubenstein 1994). A social arrangement based on reasonably satisfying the needs of both sexes is the key to forming stable social and breeding groups (harems) in Przewalski's horses (Berger 1986; Berger et al. 1999; Rubenstein 1994).

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Once a group is created, individual interactions determine the social structure or social network (Hinde 1976). These interactions can differ greatly based on the age, sex, reproductive state, personality, and life history of each individual, affecting the general structure of the group (Hinde 1976; Lehner 1996; Whitehead 2008; van Dierendonck et al. 2009). Relatedness is another important factor, it enhances proximity tolerance and promotes an increase in the number of affiliative interactions (Berger 1986), including grooming, playing, approaching another conspecific, practising head resting or head rubbing, and olfactory investigation (McDonnell & Haviland 1995; McDonnell & Poulin 2002). On the other hand, interactions that typically encourage or maintain increased distance between individuals are known as agonistic interactions (Feh 1988), which are often divided into aggressive and defensive actions (Feh 1988; Rubenstein 1994; Cozzi et al. 2010) and are commonly used to define the social hierarchy (Miller and Denniston 1979; Feh 1999). Head threats, bite threats, kick threats, biting, and kicking are examples of basic agonistic behaviors (McDonnell & Haviland 1995; McDonnell & Poulin 2002). A specific example of agonistic interaction in horses is herding. It is a behavior presented by a dominant stallion to maintain a harem and to direct its movement (King 2002; King et al. 2016).

The previously described social behaviors can be used to characterize the agonistic and affiliative social network at the group level, providing specific metrics for each individual involved (Whitehead 2008). This allows an investigation of the links between individual traits and their connections in populations where all the members are known and easily identified (Croft et al. 2008). Przewalski's horses have complex but relatively stable social networks; moreover, the current Great Gobi B population in Mongolia is composed of wild-born and captive-bred individuals with varied life experiences, all of which can be individually recognized. For these reasons, they serve as an ideal model species for analyzing social behavior and how it affects the adaptation of the animals during the reintroduction process, which is the primary goal of this study.

Several previous studies on the social behavior of horses focused primarily on the relationships among group members (Ehhardt 1957; Blakeslee 1974; Wells & Goldschmidt-Rothschild 1979; Keiper & Sambras 1986; Keiper 1988; van Dierendonck et al. 1995; Berger et al. 1999; Vervaecke et al. 2007; Bourjade et al. 2009a). However, there has not been any attempt to study groups made up of individuals with different origins (reintroduced vs. wild-born) nor to study social network differences among groups with different origins (acclimatizing vs. long-term reintroduced vs. wild-born). Such studies are surprisingly few for wild, free-roaming horses (translocated vs. born in the wild) and missing for wild-living Przewalski's horses (acclimatizing vs. long-term reintroduced vs. wild-born).

Numerous studies stressed that understanding ungulate adaptation to their environment through different aspects, including social behavior, is essential for their survival (Knight 2001; Conradt et al. 2009; Bousquet 2011; Macdonald 2016; Sniijders et al. 2017). And the lack of information on the origin, as one of the crucial factors (Berger-Tal et al. 2011) to be analyzed, became apparent. Therefore, we analyzed the impact of origin and experience on social metrics, including interaction rate, social relationships, and structure, and thus, on the formation of stable social networks in Przewalski's

horses. Along with the origin of the horses, we also tested the influence of other common factors on social network characteristics, including sex, age, relative time belonging to the group, relatedness, and dominance rank as potential sources of variability. We hypothesized that the social network measures are affected by individual traits including origin (captive breeding vs. wild-born) or the previous experience of each individual in the studied group. More specifically, we hypothesize that a higher number of interactions but weaker networks may exist between the horses at the beginning of the reintroduction process compared to lower interaction rates and strong social networks in wild-born horses. At the group level, we expect changes in the group metrics with more experience, which commonly means a reduction in the metrics' values, meaning that the roles of each individual in the group are well-defined.

Materials and Methods

Study area

The Great Gobi B Strictly Protected Area GGBSPA (established in 1975, 45°00'–26' N—91°29'–49'E) is a part of the Great Gobi Biosphere Reserve. Since 2019, it encompasses ≈18,000 km² of desert steppe and desert habitat (≈9000 km² before the enlargement, International Takhi Group, 2021). This protected area in SW Mongolia is a reintroduction site for Przewalski's horse and an important refuge for several other endangered species (Kaczensky et al. 2004; Kaczensky et al. 2008). Despite its protected area status, the GGBSPA is used by about 130 families with close to 70,000 heads of livestock, mainly in winter and during spring and fall migration (National Statistic Office of Mongolia 2021).

The climate of the GGBSPA is continental and very dry. The temperatures differ significantly during the day and night and between the seasons (cold season mean monthly temperatures vary from –20 °C to 4 °C between October and April; warm season mean monthly temperatures vary from 14 °C to 19 °C between May and September; Michler et al. 2022). The altitude ranges from 1100 to 2900 masl (International Takhi Group, 2021). The GGBSPA is situated between the Altai Mountains and the national border with China. The precipitation is within the typical range of a semi-desert climate; the annual average precipitation is 100 mm with a differentiated peak in summer (>80%; June–August). Snow cover typically lasts for around 100 days. Rain and snowfall substantially over in both time and space (Burnik Šturm et al. 2017). Drought, pronounced temperature variation, and enormous annual differences are characteristic of the habitat (International Takhi Group, 2021). The Great Gobi B SPA belongs to the central Asian plant geographical area. This region has shallow and poorly developed soils and is dominated by semi-desert and desert-steppe vegetative cover with arid-adapted plants; the most typical is *Haloxylon ammodendron*, *Ephedra przewalskii*, *Reaumuria soongarica*, *Anabasis brevifolia*, *Stipa* spp., *Artemisia* spp., and *Ajanina* spp. Plants with higher nutritional quality are frequently found in pastures with limited forage availability (Michler et al. 2022).

Data collection

Data were collected in three different seasons: summer 2018 (10 July 2018–22 July 2018), late spring 2019 (19 May 2019–23 June 2019), and autumn 2019 (10 September 2019–01 October 2019). In the summer of 2018, 3 groups were

observed (Azaa, Tsetsen, and Mares18) involving 29 individuals. In spring 2019, 4 groups were observed (Azaa, Tsetsen, Hustai1, and Mares19) involving 34 individuals. In autumn 2019, 4 groups were observed (Azaa, Tsetsen, Hustai2, and Tanan) involving 35 individuals. Specific information on the groups and individuals and their different origins (wild-born; long-term reintroduced; acclimatizing) is described in [Table 1](#) and in the [Supplementary Material](#). The season was defined in consultation with rangers of GGBSPA and local inhabitants (the herders move from winter to summer camps in spring and back in autumn). Two of the observed groups consisted of wild-born horses (born in the GGBSPA), and two consisted of reintroduced horses. The long-term reintroduced and acclimatizing horses originally come from various breeding centers in Europe and are transported to the Czech Republic into a breeding facility area from which target mares are selected and transported to the GGBSPA; part of the observation of the reintroduced groups was conducted in soft-release acclimatization enclosures (at this point, the horses were in the GGBSPA from 2 days up to 3 months after the transport from

Europe). The acclimatization enclosures are ≈500 m from the GGBSPA administration building and field station. There are four interconnected rectangle-shaped enclosures of 1.20 km², 0.33 km², 0.23 km², and 0.20 km², respectively, with natural steppe vegetation and a natural stream with water. The enclosures are fenced with 2 m high wire mesh. The smallest enclosure has a shelter consisting of three perpendicular walls with a roof. The wild-born groups were always observed in the wild ([Supplementary Material](#)). The harems were located during daily monitoring. Once one of the target harems was located, the harem was approached and filmed from 150 m to 800 m using a 4K Panasonic VX1 video camera with a tripod using the zoom function. One harem was filmed at a time, and all recordings were made by the same researcher (AB). Each group and each individual was identified by the principal researcher based on the physical feature information provided by the GGBSPA administration. Before the data collection started, the GGBSPA administration official trained the researcher to distinguish each horse. To prevent any disturbance of the horses, the least human-shy wild-born harems were selected

Table 1. Composition, experience, stability, and reproductive information of the Przewalski's horses groups studied in 2018 and 2019. Stability index indicates how similar was a group respect the previous observation period. Detailed information about the individuals composing each group is shown as [Supplementary Material](#)

Group	Season/ Year*	Observation hours	Group experience**	Individuals	Number of breeding mares	Stability index***	Age of foals (d)****
Azaa	Summer/18	18.5	wild-born	1 dominant ♂, 9 ♀, 3 ♂, 4 foals	6	0.86	46
Mares18	Summer/18	17.5	acclimatizing	4 ♀	4	0.00	–
Tsetsen	Summer/18	11.2	wild-born	1 dominant ♂, 4 ♀, 3 ♂	3	0.00	–
Azaa	Spring/19	30.0	wild-born	1 dominant ♂, 8 ♀, 2 ♂, 3 foals	5	0.83	26
Hustai1†	Spring/19	25.5	long-term reintroduced	1 dominant ♂, 4 ♀	4	0.00	–
Mares19	Spring/19	21.0	acclimatizing	3 ♀	3	0.00	–
Tsetsen	Spring/19	31.5	wild-born	1 dominant ♂, 5 ♀, 3 ♂, 3 foals	4	0.75	28
Azaa	Autumn/19	22.5	wild-born	1 dominant ♂, 6 ♀, 2 ♂, 5 foals	5	0.75	100
Tanan	Autumn/19	21.0	long-term reintroduced	1 dominant ♂, 4 ♀	4	0.00	–
Hustai2	Autumn/19	20.0	acclimatizing	1 dominant ♂, 3 ♀	3	0.00	–
Tsetsen	Autumn/19	25.0	wild-born	1 dominant ♂, 5 ♀, 3 ♂, 3 foals	4	0.75	128

Only animals older than one year (inclusive of) were used in our research. Foals are shown in the table to illustrate the general information on the studied groups.

*Summer/18 period accounts for 7 July—22 July 2018, Spring/19 Accounts For 19 May—23 June 2019 and Autumn/19 accounts for 10 September—10 October 2019.

**Group experience: acclimatizing (from 2 days up to 3 months after the transport from Europe, fenced area); long-term reintroduced (after one year acclimatization period, released); wild-born (born in the wild). One mare in the wild-born Azaa harem was born in captivity in Europe and reintroduced to the GGBSPA in 2004.

***Stability index was counted as the inter-yearly changes in the number of breeding mares (in %; the number of mares present in the group during the previous and the observation year, divided by the number of mares present in one or another year). Zeros represent groups which existed for less than 1 year.

****Average foals' age (in days) at the end of each selected observation.

†Hustai1 was created after Hustai stallion joined Mares18.

in cooperation with the local rangers. Thanks to the rangers' knowledge of each group, a sufficient distance could be maintained so as not to distract the horses or to avoid triggering flight responses. Enclosed horses were also filmed. An equivalent distance could be kept for the enclosed horses' thanks to the extensive size of the enclosures. However, these individuals were acclimated to human presence and management at the time of our data collection. The video recordings were made daily across the whole study period (in Summer, Spring, and Autumn, respectively), and each observation day was dedicated to two groups. Time from morning to afternoon or from midday to the evening was typically spent with each group. When possible, the recorded groups were changed every day, and an equal percentage of the morning-afternoon/midday-evening period was spent with each group to collect comparable data regarding environmental conditions and hours of observation. In the summer of 2018, 45 hours of recordings were collected

from three groups. In late spring 2019, 108 hours of videos were recorded from four groups. In autumn 2019, 88.5 hours of videos were recorded from four groups. The recording time was similarly distributed among all studied groups (details of recording time distributed across groups are provided in [Table 1](#)). Winter monitoring was not feasible due to low accessibility to the area (frozen paths), the technical impossibility of recording the groups due to the low temperatures.

Data processing

Behavioral Observation Research Interactive Software BORIS 7.12.2 ([Friard and Gamba 2016](#)) was used for event logging, video coding, and recording. An ethogram ([Table 2](#)) based on published material for horses ([McDonnell and Haviland 1995](#); [McDonnell and Poulin 2002](#)) and consultation with the GGBSPA administration was used to categorize the behaviors. The ethogram consisted of two categories: agonistic

Table 2. Ethogram of the behaviors recorded within this study, partially based on [McDonnell and Haviland \(1995\)](#); [McDonnell and Poulin \(2002\)](#)

Category	Behavior	Definition
Affiliative	Approach	Movement of a horse to initiate a behavior toward another horse.
	Play	The behavior appears to have no immediate use or function for the animal, involving a sense of pleasure. Various behaviors presented while playing with other individual/s.
	Grooming	Two members standing beside one another, usually head-to-shoulder or head-to-tail, grooming (each) other's neck, mane, rump, or tail by gentle nipping, nuzzling or rubbing.
	Head resting	The horse is placing its head on the other horse's body.
	Head rubbing	The horse is rubbing its head on the other horse's body.
Agonistic	Olfactory investigation	The olfactory investigation involves sniffing various parts of another horse's head and/or body. They are considered affiliative if followed by another affiliative behavior.
	Arched neck threat	Neck tightly flexed with the muzzle drawn toward the chest. Arched neck threats are observed during close aggressive encounters and ritualized interactions.
	Bite threat	No contact is made. The neck is stretched and ears pinned back as the head swings toward the target horse, warning to maintain distance.
	Bite	Opening and rapid closing of the jaws with the teeth grasping another horse. The ears are pinned, and lips retracted.
	Chase	One horse pursuing another, usually at a gallop. The chaser typically pins the ears, exposes the teeth, and bites at the pursued horse's rump and tail. The horse being chased may kick out defensively with both rear legs.
	Ears back	Ears pressed caudally against the head and neck. They were typically associated with intense aggressive interaction.
	Fight	Various behaviors are associated with fighting, not a single aggressive movement. More than one aggressive attempt must be present, including striking, rearing, mounting, lunge, levade, and repeated biting/kicking.
	Head bump	In two horses: a quick lateral toss of the head that forcefully contacts the head and neck of another horse. Usually, the eyes remain closed and the ears forward.
	Herding	Combination of a threat (usually bite) and ears laid back with forward locomotion, apparently directing the movement of another horse.
	Interference	Disruption of combat of other horses by moving between the fighting individuals, pushing, attacking, or simply approaching the combatants. One or more horses may simultaneously interfere with an encounter.
	Kick threat	Similar to a kick but without sufficient extension or force to make contact with the target. The hind leg(s) lifts slightly off the ground and under the body in tense "readiness."
	Kick	One or both hind legs lift off the ground and extend towards another horse, with apparent intent to make contact.
	Push	Pressing of the head, neck, shoulder, chest, body, or rump against another in an apparent attempt to displace the target horse.
	Retreat	A movement that maintains or increases an individual's distance from an approaching horse or a horse initiating some behavior. The head is usually low, and the ears are turned back. The retreat can be at any gait, even very slow and with little movement from the initiator.
	Snapping	Moving the lower jaw up and down in a chewing motion. A sucking sound may be made. Typically, the head and neck are extended, with the ears relaxed and oriented back or laterally.
Threat	Giving the general appearance of a warning to maintain distance. Threats are typically not directed toward the particular part of the body of another horse.	
Olfactory investigation	Involves sniffing various parts of another horse's head and/or body. Considered agonistic if followed by another agonistic behavior.	

(-Agonistic) and affiliative (-Affiliative). Other behavioral categories (feeding, lead and follow, locomotion, resting, and others) were also recorded but not used for this study. Data from BORIS were transferred to Excel. These data were further analyzed in SOCPROG 2.9 for MATLAB2018B (analysis of data on the social structure; Whitehead 2015) and DomiCalc (tools for dominance analysis; de Silva et al. 2017). In DomiCalc, only agonistic interactions were analyzed. All the other social network measures were calculated in SOCPROG separately for agonistic and affiliative behaviors.

Social network measures for individuals

Social network analysis conducted in SOCPROG allowed us to calculate the following measures: Strength, Eigenvector Centrality, Reach, Clustering Coefficient, and Affinity. Social network diagrams for agonistic (Figure 1) and affiliative (Figure 2) interactions were also prepared in SOCPROG.

Strength is the sum of association indices of any individual with all other individuals. It is counted as the sum of associations minus one. High Strength indicates that an individual strongly associates with others (Whitehead 2008).

Eigenvector Centrality measures how well an individual is associated with others and how well they are associated. Thus, to have high Eigenvector Centrality, an individual will have relatively strong associations with other individuals who have relatively strong associations (Whitehead 2008).

Reach of an individual is a measure of indirect connectedness, so the behavior of A towards B may influence the behavior of B toward C (Whitehead 2008).

The Clustering Coefficient is a measure of how well the associates of an individual are themselves associated. If all associates of an individual are linked, then the Clustering Coefficient of that individual is 1.0; if none are, it is 0.0. Clustering coefficients are high in societies containing tight, closed, homogeneous social units and lower in strict territorial societies. The Clustering Coefficient used in the SOCPROG version utilized in this research is the one of Holme et al. (2007), which states that if A is strongly connected to B and C, then B and C are also likely to have a strong connection.

Affinity is a measure of the Strength of its associates, weighted by the association index between them. Thus, an individual with high Affinity has relatively high associations with individuals with high Strength (Whitehead 2008).

Characteristics of the group social network

The group social network characteristics were calculated only for affiliative interactions and included Community division by modularity (Q) and Centralization index (CI). Community division by modularity was calculated in SOCPROG. The Centralization index was counted based on the formula provided by Ramos et al. (2019).

Community division by modularity (Q)

Association indexes are often high among individuals belonging to the same cluster and low among individuals belonging to different clusters. Community division by modularity shows that group's partition into communities. A modularity value of more than 0.3 means a strong group division (Newman 2006; Whitehead 2009).

Centralization index (CI)

It shows if and how much a network is controlled by a single or a few individuals. Centralization measures show a

network's tendency for one or a few nodes to be more central than others (Sueur et al. 2011; Griffin and Nunn 2011; Ramos et al. 2019).

Interaction rates

Interaction rates were calculated for all interactions and each interaction category (agonistic and affiliative) for each season. Rates of interactions were counted as the sum of all interactions of a given animal in a given season divided by the total number of observation hours.

Social and ecological factors

Social and ecological factors used in the analyses included: season, group, sex, age, origin, relative time belonging to the group, relatedness, and dominance rank. Season, group, sex, age, and origin (wild-born vs. captive-breed) of all individuals are described in the Supplementary Material. Only individuals over one year of age were used in our study.

Relative time belonging to the group was counted as the time in years that a given individual belonged to a group divided by the average time belonging to the group for all the group members. This relative measure was chosen over the absolute time of an animal belonging to the group to standardize the data among groups with different experiences, but also for statistical reasons (see the *Data analysis* section). The demographic information for each group and each individual was provided from the GGBSPA administration database.

Kinship was analyzed in the PMx package, which provides kinship parameters to assess relative genetic uniqueness and degree of relatedness (Ballou et al. 2020). The kinship data are determined by observation of all the harems kept in the GGBSPA administration database and the *Studbook of the Przewalski horse* (Prague Zoo, <https://przwhorse.zoopraha.cz/>). The data are based on observation, that is, the maternal relatedness is assumed by the mother/foal interaction, and the paternal relatedness is assumed by the stallion associations at the time of conception. A relatedness index was calculated for each animal as the average relatedness with all the other group mates.

Dominance rank for each member of a group was calculated with the formula: $CBI = (B + \sum b + 1)/(L + \sum l + 1)$ where B represents the number of individuals that the member defeated in one or more interactions, $\sum b$ represents the total number of individuals (excluding the member) that those represented in B defeated, L represents the number of individuals by which the member was defeated, and $\sum l$ represents the total number of individuals (excluding the member) by which those represented in L were defeated. One is added to the numerator and the denominator in the equation because some group members might not have been observed winning or losing an interaction (Clutton-Brock et al. 1979, 1982). An animal is considered defeated after showing a submissive response to displays of aggression or direct physical violence behavior aimed toward the animals by another group member (Tai et al. 2022). This approach was used for each aggression-submission bout, respectively. The behaviors considered submissive during our study are described in the ethogram (Table 2) and include Retreat and Snapping.

Data analysis

All analyses were conducted in IBM SPSS Statistics 28 (IBM, Armonk, New York). Data inspection and normality tests

were conducted, and further analyses were designed according to the characteristics of the studied variables.

A set of generalized linear mixed models (GLMMs) were designed to test the influence of the selected social and ecological fixed factors (season, group, sex, age, origin, relative time belonging to the group, relatedness index, and dominance rank) on the social network measures of the studied individuals. A first GLMM focused on understanding the factors affecting the rate of all interactions among studied horses. The second set of GLMMs focused on understanding the factors affecting the rate and social network measures of agonistic interactions of the studied horses. The last set of GLMMs was designed to test the factors affecting the rate and social network measures of affiliative interactions of all studied horses. Multicollinearity was tested through the Variance Inflation Index, which showed adequate values ($VIF < 5$) for the selected factors. The total time belonging to the group, parity (as a metric of reproductive experience), and group size had been previously excluded due to VIF values over 10. The data structure was determined by season as subject and group as a repeated measure, with ID as a random factor. Gamma response was used in all cases except for Eigenvector Centrality-Affiliative, where an Inverse Gaussian response was used. Satterthwaite approximation and robust estimation of fixed effects and coefficients were used to deal with potential violations of the model assumptions (unequal sample size in the different groups). To discard non-significant variables, the traditional stepwise backward selection procedure was used: the model was repeatedly run, excluding the less significant variable from the previous model until a final model with only significant variables was obtained. Corrected Akaike Information Criterion was used to finally select the best model, specifically when models with marginally significant variables were involved.

Median tests were used for comparing the studied behavioral indices at the group level among seasons and groups with different experiences (horses transported from Europe kept in soft-release enclosures; free-ranging reintroduced horses; free-ranging wild-born horses). We refer to the groups

in soft-release enclosures as “acclimatizing,” to free-ranging reintroduced ones as “long-term reintroduced,” and to free-ranging wild-born groups as “wild-born.”

Results

The interaction rate of all interactions decreased significantly with origin (lower in wild horses, $F = 3.758, P = 0.057, \beta = -0.510$) relative time belonging to the group ($F = 13.864, P < 0.001, \beta = -0.515$) and dominance rank ($F = 12.685, P < 0.001, \beta = -0.153$).

The rate of agonistic interaction decreased significantly with relatedness and dominance rank. Strength-Agonistic decreased with relatedness and dominance rank (Table 3). Eigenvector Centrality-Agonistic was lower for individuals with higher social rank. Reach-Agonistic decreased with age, relatedness, and dominance rank. Clustering Coefficient-Agonistic was lower in wild individuals (Figure 3) and also decreased with age. Affinity-Agonistic decreased significantly with a longer time belonging to the group and a higher degree of kinship.

The rate of affiliative interactions and Strength-Affiliative significantly decreased with relative time belonging to the group and dominance rank and were lower in wild-born horses (Table 4 and Figure 3). Eigenvector Centrality-Affiliative was lower for individuals with higher social rank, in wild-born individuals (Figure 3), and those belonging to the group for longer, but increased with age and relatedness and was higher in females. Reach-Affiliative decreased with time and dominance rank and was lower in wild-born animals (Figure 3). Clustering Coefficient-Affiliative was lower in animals with a higher degree of kinship and increased with age. Affinity-Affiliative showed significant differences in origin, relative time belonging to the group and dominance rank, being lower in wild-born animals (Figure 3), in those with a longer time belonging to the group and in dominant animals.

At the group level, social network measures and characteristics of the social network are shown in Table 5.

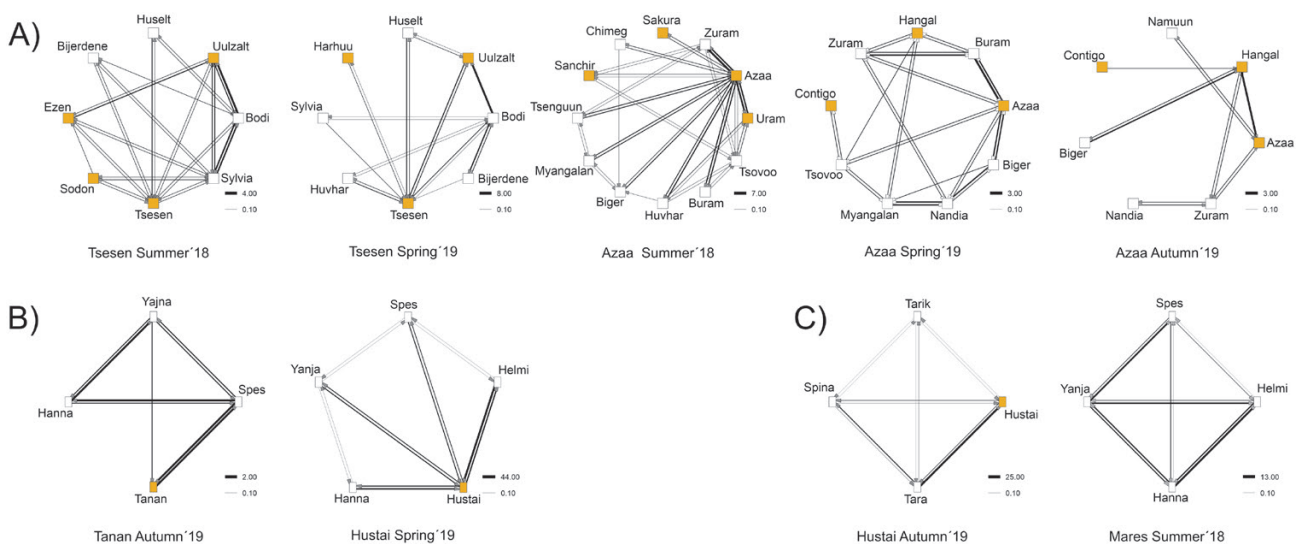


Figure 1. Social networks of the agonistic interactions within adult Przewalski's horses' group members. Females are indicated by white, and males by orange color. All the studied groups are shown grouped as wild-born (A), long-term reintroduced (B), and acclimatizing groups (C). The thickness of each dyadic interaction indicates its strength.

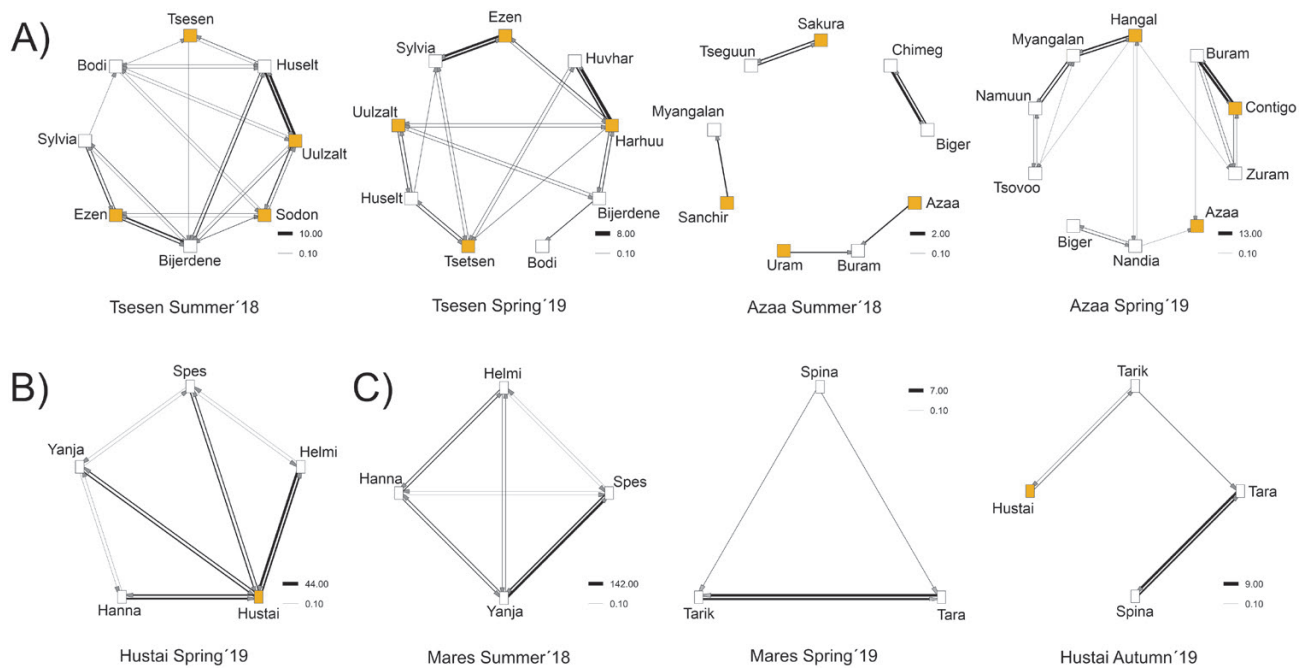


Figure 2. Social network of affiliative interactions within adult Przewalski's horses' group members. Females are indicated by white, and males by orange color. All the studied groups are shown grouped as wild-born (A), long-term reintroduced (B), and acclimatizing groups (C). The thickness of each dyadic interaction indicates its strength.

These measures were generally stable since median tests detected a low influence of season and group experience. Nevertheless, certain differences were detected. Eigenvector Centrality-Agonistic was higher for groups with high (wild-born, 0.470) and medium experience (long-term reintroduced, 0.455) compared to the groups with low experience (acclimatizing, 0.304; $M = 9.000$, $P = 0.011$). The same pattern was evident for Eigenvector Centrality-Affiliative ($M = 5.760$, $P = 0.056$), being higher in groups with high experience (0.457) compared to medium (0.350) and low experience (0.334).

Discussion

Studies reporting differences in social network metrics between groups are rare, and even more when these groups vary in terms of their experience in the context of a reintroduction program (wild-born *vs.* acclimatizing *vs.* long-term reintroduced groups). Most previous studies of the social behavior of horses focused primarily on the relationships among group members but not on the comparison of different groups of different origins (Ebhardt 1957; Blakeslee 1974; Wells and Goldschmidt-Rothschild 1979; Keiper and Sambraus 1986; Keiper 1988; van Dierendonck et al. 1995; Berger et al. 1999; Vervaecke et al. 2007; Bourjade et al. 2009a). The rate of interactions and Strength are highly connected, and the models showing the variables affecting them were remarkably similar; thus, these two measures are discussed together.

The results confirmed our hypothesis: horses' origin (captive-breeding *vs.* wild-born) strongly influences the social network at agonistic (Table 3) and affiliative (Table 4) levels. For agonistic interactions, origin affected the Clustering Coefficient-Agonistic, which was lower in wild-born individuals (i.e., the network density in terms of aggressiveness was

lower for wild-born horses of our study). This result agrees with previous studies revealing that in stable groups, the hierarchy between horses is set, and the knowledge of the dominance status of group mates makes new challenges unnecessary (Berger 1977; Wells & Goldschmidt-Rothschild 1979; Heitor et al. 2006). One limitation of the study is that only wild-born animals were observed exclusively in free-ranging conditions, while reintroduced individuals were observed both in enclosures and free-ranging. The lower Clustering Coefficient-Agonistic in wild animals in our study is in line with previous studies suggesting that horses in enclosed areas display higher aggression rates (Keiper & Receveur 1992).

Origin strongly affected most social network metrics based on affiliative interactions (Table 4). The lower Strength-Affiliative and rate of affiliative interactions observed in wild-born horses confirm previous observations by Feh and Carton de Graumont (1995), who stated that new groups display more affiliative interactions than stable groups of horses. Weaker affiliative connections and network densities were also found in wild-born animals compared to the captive-bred ones (lower Eigenvector Centrality-Affiliative, Reach-Affiliative, and Affinity-Affiliative). These results indicate the existence of well-established roles among the group members for wild-born horses, not needing continuous reinforcement. Some of our captive-bred individuals were observed shortly after transportation from Europe. Thus the higher occurrence of affiliative interactions and Strength-Affiliative (as well as higher Eigenvector Centrality-Affiliative, Reach-Affiliative, and Affinity-Affiliative) among them could also be interpreted as a stress-reducing behavior (Hogan et al. 1988). A low indirect connectedness was found in wild-born horses (low Affinity-Friend); in other words, lower "behavioral contagion," which is also typical for stable groups. Altogether, the results suggest that forming complex stable relationships requires time; thus, such a process may be essential for the

Table 3. General linear mixed models (GLMMs) assessing the factors affecting the rate and social network measures of agonistic interactions of all studied Przewalski's horses. Solved models after a backwards selection process are shown

Factor	Interaction rate	Strength	Eigenvector Centrality	Reach	Clustering Coefficient	Affinity
Sex	–	–	–	–	–	–
Age	–	–	–	$F = 5.586, P = 0.022, \beta = -0.075$	$F = 6.645, P = 0.013, \beta = -0.038$	–
Origin*	–	–	–	–	$F = 9.127, P = 0.004, \beta = -0.445$	–
Time in group	–	–	–	–	–	$F = 7.797, P = 0.007, \beta = -0.313$
Relatedness	$F = 10.833, P = 0.002, \beta = -4.840$	$F = 14.021, P < 0.001, \beta = -5.225$	–	$F = 72.966, P < 0.001, \beta = -13.330$	–	$F = 39.447, P < 0.001, \beta = -6.063$
Rank	$F = 7.218, P = 0.009, \beta = -0.127$	$F = 6.394, P = 0.014, \beta = -0.113$	$F = 16.767, P < 0.001, \beta = -0.094$	$F = 6.744, P = 0.012, \beta = -0.147$	–	–

Dashes indicate variables which were discarded during the model solving process due to their lack of significance. Thus, these variables were not included in the final models shown in the table.

*Captive-breeding origin was used as the category of reference. Therefore, positive β means higher values in wild animals compared with reintroduced ones.

long-term success of the reintroduction program (Gusset et al. 2010; Gaudioso et al. 2011).

Beyond the horses' origin, other factors affected the social networks for agonistic and affiliative interactions. The Strength-Agonistic and the rate of agonistic interaction significantly decreased with dominance rank and kinship (Table 3). Various studies have reported opposite results: regardless of their weight, height, sex, or time belonging to the group, aggressive horses attain higher ranks than passive horses (fenced: Ebhardt 1957; free-ranging: Blakeslee 1974; Keiper and Receveur 1992). However, findings of other studies align with our results, suggesting that the most aggressive horses are not usually the most dominant (Berger 1986; Feh 1988; van Dierendonck et al. 1995; Bourjade et al. 2009b). We interpret reduced aggression in high-ranking animals in our study is caused by the fact that once the hierarchy is formed (stable harems), it is maintained without the necessity of continuous aggressive interactions (Berger 1977; Wells and Goldschmidt-Rothschild 1979).

Regarding kinship, low aggression between relatives has been observed in other social ungulates like red deer (Ceacero et al. 2007). In feral horses, Heitor et al. (2006) found no effect of kinship on aggressive behavior, and Boyd and Houpt (1994) stated that closely related Przewalski's horses are typically less aggressive towards each other than towards more distantly related individuals. Moreover, high-ranking horses did not have strong, aggressive associations with individuals who have strong associations themselves. Results thus suggest that the affiliative bonds among relatives become essential in harsh environments for reducing stress (Hogan et al. 1988).

Clustering Coefficient-Agonistic decreased with age, and Reach-Agonistic decreased with age, relatedness, and dominance rank, meaning that older animals, those with relatives in the group, and high-ranked ones show low indirect connections regarding agonistic behaviors, again typical of stable groups (Table 3). The horse's social position in the group is highly correlated with its age (Houpt et al. 1978; Keiper and Sambras 1986; Keiper and Receveur 1992; Linklater et al. 1999), which may also explain these results. Animals belonging to the group for a longer time and animals with a higher degree of kinship were less likely to be aggressive towards

very aggressive individuals (lower Affinity-Agonistic; Table 3).

Strength-Affiliative significantly decreased with relative time spent in the group and higher dominance rank. Older animals, more closely related animals, and females had stronger associations with individuals who also have strong associations (higher Eigenvector Centrality-Friend; Table 4). Friends of related and older horses were more likely to be friends also with each other. Less dominant animals were more likely to associate with individuals who have strong associations. Previous studies found no link between time belonging to a group and the occurrence of allogrooming, nor between affiliative interactions and dominance rank (Clutton-Brock et al. 1976; King and Gurnell 2019). However, a negative correlation between affiliative behaviors and a horse's dominance rank was reported by Keiper and Receveur (1992). It has been proven that affiliative behavior, especially allogrooming, might be costly for the donor (tooth attrition, loss of water in saliva, reduction in feeding, or reduction in vigilant behavior; Mooring and Hart 1995; Henzi and Barrett 1999). For this reason, it could be exchanged for other social benefits, including tolerance from more dominant individuals or maintaining social bonds (Henzi and Barrett 1999; Gumert 2007; Schino 2007). In severe environmental conditions such as in the Mongolian Gobi, group living is highly connected to the fitness of equids and may even be vital for their survival (Zhang et al. 2015; Gersick et al. 2017). Therefore, the negative correlation of dominance rank and affiliative interactions among horses in our study might be driven by the "trade-off hypothesis," indicating that subordinates exchange allogrooming (and other affiliative behaviors) to be tolerated in the group and develop and preserve social bonds with more dominant horses. Indeed, adult horses show little allogrooming rate (Crowell-Davis et al. 1986). Another explanation might be connected to the need for appeasement or reconciliation as in group living horses, where affiliative reunions often serve as mechanisms of non-dispersive conflict resolution (Cozzi et al. 2010). In this case, reconciliation would be directed by subordinates toward more dominant horses, which might use grooming (or other affiliative interactions) to appease higher-ranked animals (Keiper 1988).

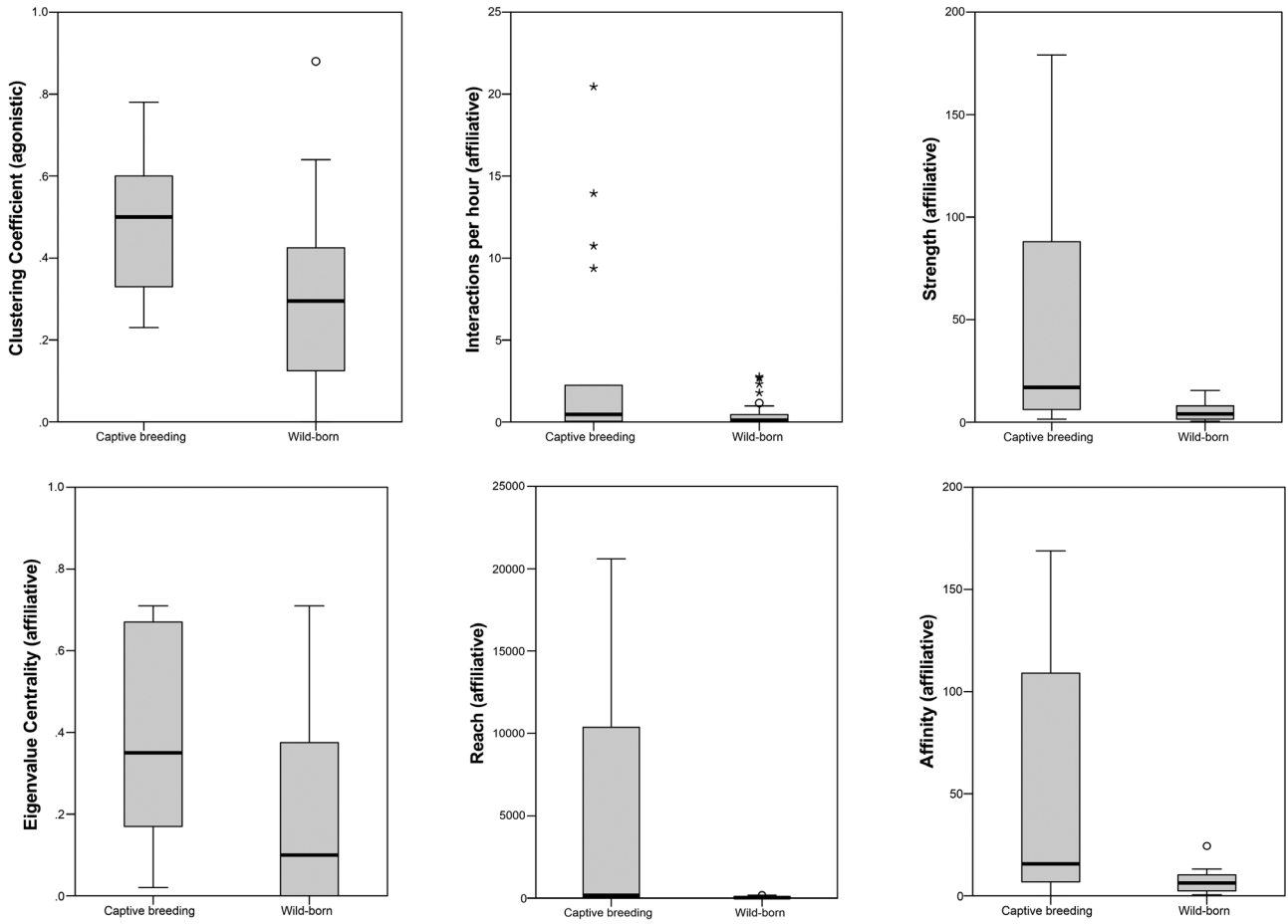


Figure 3. Differences in agonistic (top-left figure) and affiliative (rest of the figures) interaction rates and social network measures in the studied Przewalski’s horses according to their origin (captive-breeding vs. wild-born)..

Table 4. General linear mixed models (GLMMs) assessing the factors affecting the rate and social network measures of affiliative interactions of all studied Przewalski’s horses. Solved models after a backwards selection process are shown

Factor	Interaction rate	Strength	Eigenvector Centrality	Reach	Clustering coefficient	Affinity
Sex*	ns	ns	$F = 10.282, P = 0.003, \beta = 0.086$	ns	ns	ns
Age	ns	ns	$F = 7.682, P = 0.009, \beta = 0.016$	ns	$F = 4.008, P = 0.054, \beta = 0.06$	ns
Origin**	$F = 6.028, P = 0.017, \beta = -0.953$	$F = 14.348, P < 0.001, \beta = -1.459$	$F = 5.211, P = 0.029, \beta = -0.340$	$F = 49.953, P < 0.001, \beta = -3.457$	ns	$F = 18.103, P < 0.001, \beta = -1.366$
Time in group	$F = 18.413, P < 0.001, \beta = -0.966$	$F = 19.626, P < 0.001, \beta = -1.041$	$F = 12.197, P = 0.001, \beta = -0.306$	$F = 27.657, P < 0.001, \beta = -1.516$	ns	$F = 11.252, P = 0.002, \beta = -0.633$
Relatedness	ns	ns	$F = 13.842, P < 0.001, \beta = 3.100$	ns	$F = 8.673, P = 0.006, \beta = -3.732$	ns
Rank	$F = 4.364, P = 0.042, \beta = -0.128$	$F = 4.475, P = 0.047, \beta = -0.119$	$F = 12.184, P = 0.001, \beta = -0.530$	$F = 8.625, P = 0.005, \beta = -0.214$	ns	$F = 11.115, P = 0.002, \beta = -0.159$

ns: not significant.

*Male sex was used as category of reference. Therefore, positive β means higher values in females compared with males.

**Captive-breeding origin was used as category of reference. Therefore, positive β means higher values in wild animals compared with reintroduced ones.

Table 5. Social network measures and characteristics of the group social network at the group level for all the Przewalski's horses groups studied. A full description of each measure can be found in the methods section.

Period	Group	Measure	Strength	Eigenvector centrality	Reach	Clustering coefficient	Q*	CI (%)**
Summer/18	Azaa	Agonistic	7.67	0.25	124.17	0.34	0.84	65.56
		Affiliative	0.89	0.16	0.94	0.00		
Summer/18	Tsetsen	Agonistic	5.50	0.32	37.56	0.36	0.38	44.58
		Affiliative	9.00	0.27	103.62	0.17		
Summer/18	Mares18	Agonistic	18.50	0.49	355.13	0.59	0.38	36.84
		Affiliative	119.25	0.48	15621.25	0.29		
Spring/19	Azaa	Agonistic	4.33	0.31	21.50	0.21	0.67	62.79
		Affiliative	7.50	0.17	80.90	0.15		
Spring/19	Tsetsen	Agonistic	6.38	0.31	60.00	0.45	0.48	46.00
		Affiliative	5.55	0.28	37.94	0.05		
Spring/19	Hustai1	Agonistic	43.20	0.42	2795.20	0.49	0.47	53.70
		Affiliative	14.80	0.35	307.70	0.23		
Spring/19	Mares19	Agonistic	–	–	–	–	0.50	37.78
		Affiliative	4.33	0.51	24.33	0.39		
Autumn/19	Azaa	Agonistic	2.14	0.33	6.57	0.24	–	46.8
		Affiliative	–	0.79	7.77	4.40		
Autumn/19	Tsetsen	Agonistic	–	–	–	–	–	–
		Affiliative	–	–	–	–		
Autumn/19	Tanan	Agonistic	3.25	0.49	11.13	0.46	–	–
		Affiliative	–	–	–	–		
Autumn/19	Hustai2	Agonistic	16.00	0.45	316.25	0.42	0.56	53.04
		Affiliative	5.00	0.38	34.25	–		

Dashes indicate measures that could not be calculated due to a low number of interactions performed by the horses at that group and period.

* Community division by modularity.

** Centralization index.

Clustering Coefficient-Affiliative decreased with kinship, but Eigenvector Centrality-Affiliative increased with a higher degree of relatedness in affiliative interactions in our study. To have high Eigenvector Centrality, individuals have relatively strong associations with others who also have relatively strong associations (Whitehead 2008). This result is in line with the study of Heitor et al. (2006), who found that kinship significantly affects the affiliative behaviors of horses; bonds are reciprocal and more robust among horses with higher relatedness and with Van Dierenonck et al. (2004), who observed a positive correlation between kinship and allogrooming. We assume that this result might be caused by the fact that horses do not choose their friends based on relatedness but also a close acquaintance or knowledge of other group members (Monard et al. 1996; Linklater 2000).

Sex did not influence the majority of the network measures of our study. It only affected Eigenvector Centrality-Affiliative, which was higher in females. Keiper and Receveur (1992) also found that females initiated most allogrooming events in a group of Przewalski's horses in a semi-reserve. We assume that affiliative behavior between mares in our study provides harem cohesiveness independent of the stallion, as described by Crowell-Davis et al. (1986).

Contradictory to previous research, we observed no effect of seasons on the social network measures of our study. Previous studies detected the season's influence on affiliative and agonistic interactions. King and Gurnell (2019) found a prevalence of affiliative interactions in the spring season, and

Tyler (1972) and Kimura (1998) observed the most associative interactions in the summer. It is noted that winter monitoring was not possible due to low accessibility to the area (frozen paths) and the technical impossibility of recording the herds due to the low temperatures. For this reason, we emphasize a need for further research concerning all seasons (including winter).

At the group level, we detected no influence of experience on the affiliative and agonistic interaction rates of the studied groups, and the social network measures were relatively stable. Nonetheless, the experience influenced Eigenvector Centrality-Agonistic, indicating high aggressiveness toward group mates who are also highly aggressive. It was higher in groups with high (wild-born) and medium (long-term reintroduced) experience compared to the groups with low experience (acclimatizing). Similarly, Eigenvector Centrality-Affiliative indicating strong associations with highly associative group mates was marginally higher in groups with high experience compared to medium and low experience. It is exciting to interpret these results in connection with the results obtained at the individual level: while wild-born groups have well-defined social networks (see Figures 1 and 2) and strong association indices, wild-born individuals have weak ones. In other words, members of wild-born harems do not need to display many agonistic or affiliative behaviors to maintain a group with strong social metrics. On the contrary, groups composed of on captive-born individuals are highly interactive both in terms of agonistic and especially affiliative interactions.

It should be noted that three groups (Mares18, Mares19, and Hustai2) were observed exclusively in their enclosures. Moreover, the Mares19 group was observed just three days after transportation to Mongolia. Even if the enclosures are large enough to allow the animals not to be disturbed by human presence, the behavior of these horses could have been influenced by these factors (transportation, semi-captivity). Similarly, more extended recording of more groups would have yielded more robust results; thus, extended monitoring of different types of groups is strongly recommended.

In summary, all the individual and group-level results indicate that experienced groups composed of wild-born individuals are more strongly socially connected than newly formed groups based on reintroduced individuals. The transition from the soft-released to the wild-born groups clearly shows more robust networks with lower interaction rates in line with previous studies describing the noticeable acclimatization period during which released horses gradually switch to the behavioral patterns of wild horses (Scheibe et al. 1997; Boyd and Bandi 2002). Indeed, our previous results in these same groups also show that wild-born harems are better adapted to deal with changing weather conditions than reintroduced ones (Bernátková et al. 2022). As the population of Przewalski's horses in Mongolia grows, understanding its behavior becomes increasingly vital and may aid in improving the reintroduction program. Przewalski's horses not only require an acclimatization period in the enclosure to adapt to the local environmental conditions but also to form social relationships through a high rate of interactions during this period. Long-term monitoring of the behavioral ecology of released Przewalski's horses released to novel habitats is thus essential to ensure a successful reintroduction.

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Authors' Contributions

AB, FC, MK, GO, and JŠ conceived the ideas and designed the methodology; AB and FC collected and processed the data; FC and AB analyzed the data; AB and FC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supplementary Material

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

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