BEHAVIOURAL MECHANISMS OF SOCIAL COHESION IN GROUPS OF REINTRODUCED TAKHI (PRZEWALSKI'S HORSE, *EQUUS FERUS PRZEWALSKII*) IN MONGOLIA

HANNAH S. DAVIE

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Abstract

Reintroduction of an endangered species or subspecies is only the first step towards ensuring survival and population increase. The first phase of takhi (*Equus ferus przewalskii*) reintroductions has been successful, but populations remain at risk from isolation, resource competition with humans and livestock, and hybridisation with modern domestic horses. Greater social cohesion in takhi family groups reduces the risk of individual and group isolation and of hybridisation, which in turn increases the integrity and vigour of reintroduced populations. The aim of this study was to investigate potential behavioural mechanisms of social cohesion in reintroduced takhi, exploring mechanisms of cohesion both within and between family groups. Interindividual spatial distribution served as a surrogate measure of cohesion, and potential mechanisms included interindividual interactions and differences in individual reproductive state, personality, and group membership. Social network analysis was used to identify classes of takhi significantly central to spatial and interaction networks. Two repeatable personality traits were detected (sociability and assertiveness), but reproductive state had a stronger influence on cohesion than did personality. Mares were the most active managers of intragroup spatial distribution. Stallions were the most active managers of intergroup cohesion. Stallions and colts were most active in intergroup affiliative networks. Overall, reproductive state most clearly dictated individual involvement in interactions influencing intra- and intergroup cohesion, while group membership and personality influenced intergroup spatial cohesion. This study is the first to incorporate personality assessment and fine-scale spatial data into an investigation of Type I equid social structure in naturally established, free-living takhi family groups. Future takhi management efforts should focus on monitoring interstallion relationships, colt social development, and filly dispersal as the primary sources of variation and changes in group and herd level cohesion in takhi populations. Results of this study can be applied to adaptive management of takhi populations, and groups and herds of other Type I equids, including feral and domestic horses.

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1. Introduction

1.1. Introduction

Takhi (also known as Przewalski's horse, *Equus ferus przewalskii*) represent hope for the future of wildlife conservation through their return to the wild after near extinction. However, most of the anthropogenic pressures that nearly drove takhi to extinction have only increased in recent decades. For takhi to remain wild, with free-living and self-sustaining populations, managers need to be able to understand and predict how takhi, as populations, groups, or even individuals, will respond to the unavoidable pressures brought by the presence of humans and livestock.

The overall aim of this study is to explore how the behaviour, characteristics, and relationships of individual takhi shape the social structure of groups and herds in reintroduced populations in Mongolia. Takhi have a dynamic social structure where the needs of each individual contribute to the behaviours and relationships seen within and between different social groups. Understanding how individual takhi vary in their social behaviour and how these variations in behaviour shape the structure of groups and herds provides valuable tools for management. The interactions of individuals form the foundation of species' social structure. In the small and isolated populations of the endangered and highly social takhi, the actions and relationships of each individual have a proportionally greater impact on higher level social structure. Social structure in turn shapes patterns of mortality, reproduction, and dispersal (Whitehead 2008a), which are themselves central drivers of the relative health and resilience of populations of interest (Ransom et al. 2016). This study will explore the social structure of family groups (a stallion, one to several mares, and their offspring, see section 1.6.4 for additional detail) in two populations of reintroduced takhi, and will investigate the role of variation in individual takhi characteristics in shaping intragroup and intergroup cohesion.

1.2. The importance of large ungulate conservation

Large terrestrial herbivores, those >100 kg (Ripple et al. 2015), are prominent among the charismatic megafauna that have for years attracted the attention and admiration of humans of all ages and from all walks of life. Consequently, they often serve as flagship or umbrella species for conservation work (Walpole and Leader-Williams 2002). Large herbivores can bring goods and income to rural communities, either directly through harvesting or indirectly by attracting business and investments to the area, particularly in areas with a healthy ecotourism industry (Gordon et al. 2004). They are also ecologically important as ecosystem engineers, seed dispersers, and nutrient cyclers, and as food sources for predators, including humans (Ripple et al. 2015). Despite their value to many humans and their importance to ecosystem functions, the world's largest terrestrial herbivores are facing significant population declines and range contractions around the globe (Ripple et al. 2015). Of the 74 largest terrestrial herbivore species, 44 are listed by the International Union for the Conservation of Nature (IUCN) as threatened with extinction, and 43 of the 74 have populations that are decreasing (Ripple et al. 2015, IUCN 2016).

1.2.1. Causes of large herbivore decline

The fundamental cause of large herbivore declines is an exponentially increasing human population and the increasing human consumption of resources per capita (Ripple et al. 2015). Major subcategories of threats to large herbivores include hunting and over-harvest by humans, shifts in human land use patterns, space and resource competition with livestock, and climate change (Christensen et al. 2004, Gordon et al. 2004, Vavra et al. 2007, Luo et al. 2015, Ripple et al. 2015). Work is being done around the world to facilitate slower human population growth and regulate extremes of resource consumption, but conservation efforts for the immediate future need to include strategies that are effective despite increasing human population density (Ripple et al. 2015).

1.2.2. Reintroduction as an important tool for large herbivore conservation

Reintroduction, the 'intentional movement and release of an organism inside its indigenous range from which it has disappeared' (IUCN/SSC 2013) is a conservation method that can bring species back from the brink of extinction, restore ecosystem functions, and combat global trends in biodiversity loss (Sarrazin and Barbault 1996, Fischer and Lindenmayer 2000, IUCN/SSC 2013). Reintroductions and translocations represent fairly drastic conservation measures. The positive and negative consequences of reintroduction affect not only the species reintroduced, but also other species, including humans, in and around the release site and the structure and function of the surrounding ecosystem (IUCN/SSC 2013, Zukosky 2016).

Important landmarks for reintroduction success include the survival of released individuals, successful reproduction by released individuals and their offspring, and the continued persistence of the reintroduced population over time (Seddon 1999). The first two landmarks can usually be clearly identified. The last, only through long-term monitoring of the reintroduced population (Sarrazin and Barbault 1996, Seddon 1999, Fischer and Lindenmayer 2000, IUCN/SSC 2013). Although the fundamental objective of all reintroduction efforts is the establishment of a self-sustaining population, maintaining that state may necessitate post-release intervention and regular reassessment of the status of the reintroduced population (Seddon 1999).

An important part of long term monitoring of reintroduced populations is the research and monitoring of behaviour and the social structure (Berger-Tal et al. 2011, IUCN/SSC 2013, Nelson 2014). Monitoring the movement, spatial use, foraging patterns, vigilance behaviour, social structure, and reproductive behaviour of reintroduced individuals can provide behavioural indicators of the health of the reintroduced population and the ecosystem in which they live (Berger-Tal et al. 2011). Behaviour monitoring and research can also be used to develop management plans that incorporate knowledge of how behaviour influences population dynamics and viability (Anthony and Blumstein 2000, Berger-Tal et al. 2011). The social structure of some species, including equids, can lead to effective population sizes (N_e) that are much smaller than the number of adult individuals in the population (Anthony and Blumstein 2000, Uzans et al. 2015). Behaviour traits that can influence N_e include mating systems and mechanisms of mate choice that limit the number of reproducing adults, reproductive behaviours that require special resources, reproductive suppression, sexually selected infanticide, social plasticity, and patterns of dispersal and migration (Anthony and Blumstein 2000). Understanding how the behaviour traits and behavioural plasticity of a species, and even the cultures of a reintroduced population, influence N_e can be critical for designing effective management strategies.

1.2.3. Equid conservation challenges

Equid reintroductions present fewer challenges than other taxa in some aspects of reintroduction, as they are generally resilient and adaptable and are capable of surviving in a wide range of habitats, ranging from arid deserts to temperate forests (King 2002, Schoenecker et al. 2016). However, equids are also large-bodied, with home ranges for social groups ranging from 0.75 to 69,988 km^2 depending on species, season, and habitat quality (King 2002, Kaczensky et al. 2011, Schoenecker et al. 2016). They have complex social structures which decrease N_e and a slow rate of reproduction (Ransom et al. 2016). Thus, some aspects of equid behaviour and ecology present additional challenges to reintroduction efforts.

1.3. Takhi as a conservation success

Prior to their extinction, takhi were last seen in the wild in 1969 (Bouman and Bouman 1994). The final extinction of the dwindling population was driven by a combination of hunting pressure from humans, resource competition with humans and livestock, and a series of harsh *zud* (also spelled '*dzud*') winters (Bouman and Bouman 1994). *Zuds* are characterised by summer drought followed by extremely cold and snowy winters that often cause high mortality among wildlife and livestock (Kaczensky et al. 2011). Takhi were listed as Extinct in the Wild until the early 1990s, when the first individuals were reintroduced to Mongolia

(Bouman and Bouman 1994, King, Boyd, et al. 2015). After reintroduction, they were downgraded from Extinct in the Wild to Critically Endangered in 2008 (King, Boyd, et al. 2015). Successful establishment of reintroduced populations with more than 50 adult individuals living wild led to a further downgrade to Endangered in 2011 (King, Boyd, et al. 2015).

1.3.1. Species description

In appearance, adult takhi resemble stocky horses of 13 to 14 hands in height (132 – 142 cm), usually weighing 240 to 300 kg (Groves 1994). Typical takhi colouration is dun with black points and a dorsal stripe running down the back. The shades of dun can range from a very light dun to a deep bay (Figure 1.1).

Figure 1. 1. The general appearance and colour variation of takhi

1.3.2. Takhi taxonomy and status as a subspecies

Current nomenclature lists takhi as a subspecies of *Equus ferus* in the family Equidae, Order Perissodactyla. They have previously been described as their own species, *Equus przewalskii* (Poliakov, 1881). Domestic horses were also originally their own species (*Equus caballus*) but were renamed as a subspecies of *Equus ferus* (*Equus ferus caballus*) in response to 2003 bulletin issued by the International Commission on Zoological Nomenclature (ICZN 2003). Although takhi have a chromosomal karyotype (2n=66) which is different from that of domestic horses (2n=64), the two species can interbreed and produce fertile hybrids (Boyd and Houpt 1994, Goto et al. 2011). Studies of takhi genetics have confirmed that modern domestic horses are not descended from takhi, but they do share a common ancestor. The two subspecies diverged an estimated 38,000 – 72,000 years ago (Der Sarkissian et al. 2015), long before the first evidence of horse domestication, dated at ~5,500 years ago (Outram et al. 2009). Recent studies have proposed that takhi are not truly wild, but are the feral descendants of horses domesticated by the Botai ~5,500 years ago, while modern domestic horses are descended from horses domesticated at a later date by different cultures (Gaunitz et al. 2018). Further research is necessary confirm the descent of modern takhi and domestic horses.

All living takhi today are descended from 12 takhi founders. The first 11 takhi founders were foals captured in southwest Mongolia between 1901 and 1903. The last takhi founder, Orlitza III, was captured in Mongolia in 1947 (Boyd and Houpt 1994, Bowling et al. 2003). One Mongolian domestic horse mare was known to be a 13th founder from the beginning of the captive breeding programme (Boyd and Houpt 1994, Miller 1995). Recent genetic analyses have now identified up to three previously unknown domestic horse founders (Der Sarkissian et al. 2015).

The small size of the founding population has led to ongoing concern among captive breeding programmes over how to minimise the effect of the known introgression of domestic horse genes and manage high levels of inbreeding. Although the loss of genetic distinctiveness through hybridisation with domestics remains a serious concern for reintroduced takhi, evidence of gene flow between the two subspecies for thousands of years prior to the captive breeding programmes (Goto et al. 2011, Der Sarkissian et al. 2015) suggests that modern takhi can still be considered a distinct and viable subspecies of *Equus ferus*.

1.3.3. Reintroduction of takhi to the wild

From the original founders (takhi and domestic), the modern takhi population has now increased to over 2000 individuals worldwide (Der Sarkissian et al. 2015). Today, in addition to the individuals in zoos and breeding centres, there are takhi populations in semi-reserves in Ukraine, Hungary, Uzbekistan, and France (Table 1.1.; Bahloul et al. 2001, King, Boyd, et al. 2015, Brindley 2016).

Table 1. 1. Location and estimated population size of free ranging or semi-free ranging takhi populations around the world.

Location	Number of Individuals	Year of population count	Reserve size (km^2)	Source
Dunhuang Xihu National Nature Reserve, China	28	2012	6600	(Liu et al. 2014, King, Boyd, et al. 2015)
Kalamaili Nature Reserve, China	127	2013	17330	(King, Boyd, et al. 2015, Kaczensky et al. 2016)
Le Villaret, Cevennes National Park, France	24	2015	3.8	(Association pour le cheval de Przewalski: TAKH 2016a)
Hortobágy National Park, Hungary	254	2014	700	(King, Boyd, et al. 2015)
Hustai National Park, Mongolia	318	2014	570	(Usukhjargal 2014)
Seer, Khomyn Tal, Mongolia	68	2016	140	(Association pour le cheval de Przewalski: TAKH 2017a)
Takhiin Tal and Takhiin Us, Great Gobi B Special Protected Area, Mongolia	132	2015	9000	(Burnik Sturm et al. 2017)
Orenburg Nature Reserve, Russia	20	2016	166	(Арсеничеб 2016, Brindley 2016)
Askania Nova, Ukraine	70	2014	30	(King, Boyd, et al. 2015)
Chernobyl exclusion zone, Ukraine	~60	2014	2600	(King, Boyd, et al. 2015)
Bukhara, Uzbekistan	37	2008	51	(King, Boyd, et al. 2015)

The first takhi reintroduction projects were initiated in 1990, at Hustai National Park (Hustai) in the central Mongolian steppe and at Takhiin Tal in the Great Gobi B Special Protected Area (GGB) in the Dzungarian Gobi (Figure 1.2; Kaczensky et al. 2016). The third Mongolian reintroduction at Seeriin Nuruu (Seer) in Khomyn Tal started in 2004 (Figure 1.2; Kaczensky et al. 2016). Reintroduction efforts are now also underway in China, Kazakhstan, and Russia (Table 1.1.).

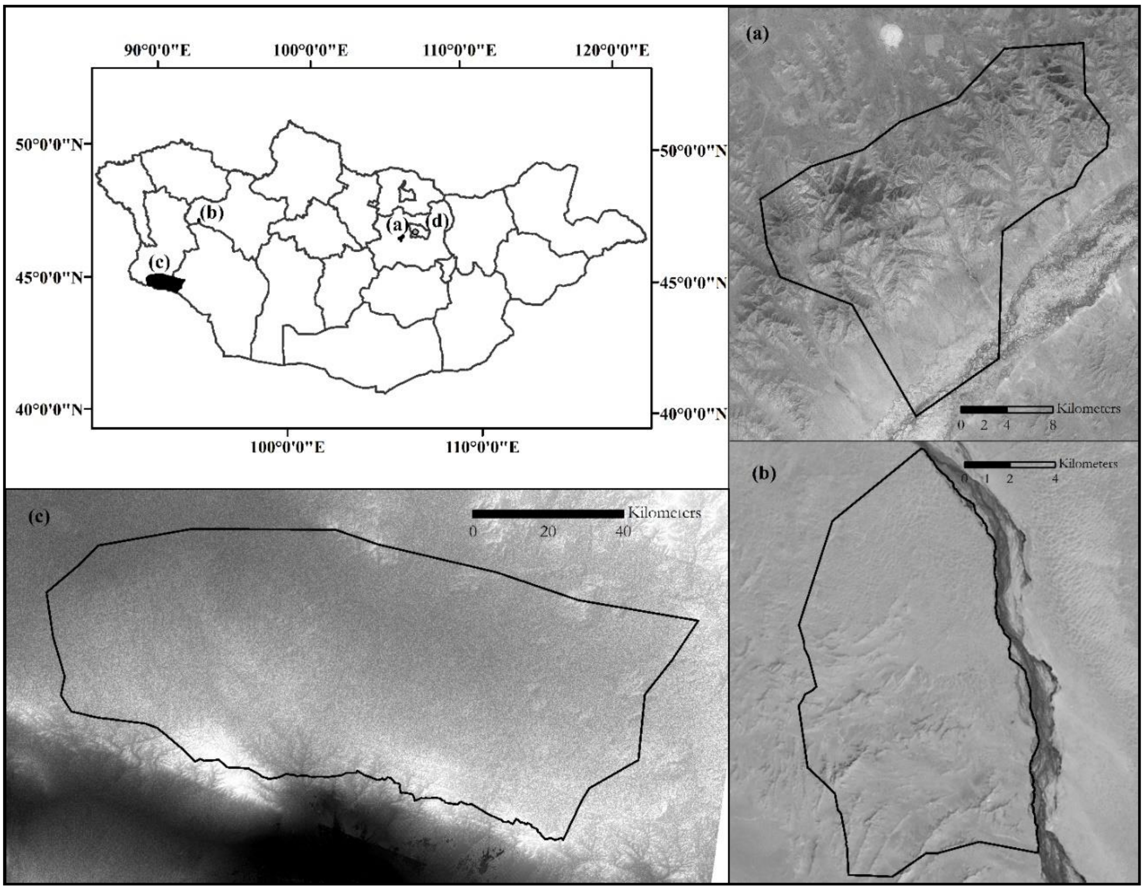


Figure 1. 2. Sites of Mongolia takhi reintroduction projects at (a) Hustai National Park, (b) Seer in Khomyn Tal, and (c) the Great Gobi B Special Protected Area, and (d) the location of the capital city, Ulaanbaatar.

1.4. An overview of reintroduction projects at study sites in Mongolia

Research for this study was conducted at two of the three Mongolian reintroduction sites. Seer was the primary research site, and Hustai was the secondary research site.

1.4.1. Seer, Khomyn Tal: site description and overview of reintroduction efforts

Seer (47.83° N, 94.11 ° E) is a fenced area of 140 km^2 located in the southeast corner of the Khomyn Tal livestock management unit in Onts *bag*, Duruljiin *sum*, in Zavkhan *aimag* (Figure 1.2b; Joly et al. 2012). The site is located at an elevation of 1300 m in the semi-desert steppe vegetation zone (Hilbig 1995 in Joly et al. 2012), with the Gobi Desert to the south, the Altai mountains to the west, and the Khangai mountains to the east. Mean annual temperature ranges from -2 to 4 ° C and annual precipitation between 50 and 100 mm (Tsegmid and Vorobev 1990 in Joly et al. 2012).

Prior to their reintroduction to the chosen location at Seer, takhi were first brought to a semi-reserve in Le Villaret in the Cevennes National Park in southern France (44.25° N, 3.44° E) in 1993. At Le Villaret the takhi were allowed to form natural social groups and to learn to survive without supplemental feeding and with minimal human intervention (Association pour le cheval de Przewalski: TAKH 2015). Le Villaret's founding population consisted of takhi brought from eight European Zoos (Tatin et al. 2009). The population, which reached 55 individuals in 2003, remained closed until the first shipment of takhi to Mongolia (Tatin et al. 2009). The first of the two shipments from Le Villaret to Seer consisted of two bachelor colts and two naturally established family groups, the first with a stallion, four young mares and a yearling colt, and the second consisting of a stallion, two mares, and a yearling filly (Association pour le cheval de Przewalski: TAKH 2016a). The second shipment consisted of another bachelor colt and two more pre-established family groups, the first with a stallion, three mares of varying ages, and a two-year-old colt, and the second with a stallion, two mares, and the two-year-old filly (Association pour le cheval de Przewalski: TAKH 2016b). An additional three mares and one stallion came from the Prague Zoo in 2011. Population growth at Seer was initially slow, largely due to the delayed reversibility of the contraceptive PZP administered to all mares older than one year (n=12) prior to transport (Feh 2012a). The first foals to survive to independence were born in 2008 (Association pour le cheval de Przewalski: TAKH 2016b). Since 2008 the population has continued to increase, reaching 60 individuals in four family groups with 15 additional bachelors in the summer of 2016 (Feh, pers. comm. 2016; Drouard, pers. comm. 2016). Of the 60 individuals, 18 (30%) were mares, three (5%) stallions, 10 (16.7%) fillies, 20 (33.3%) colts, and 9 (15%) foals (both sexes).

Within the reserve, the Seer takhi usually graze in the *Stipa spp.* dominated pasture in the mountain foothills. They are most active in the morning and evening, and rest through the midday period. In summer, midday rest usually occurs under artificial shelters or on sand or bare rock, and in winter, on sunny slopes. In summer, the takhi make daily trips down to drink at the river. In the winter, they use snow as a water source.

1.4.2. Hustai National Park: site description and overview of reintroduction efforts

Hustai, (47.69° N, 105.87° E) is a 570 km^2 Strictly Protected Area (SPA) located in Tuv *aimag,* 150 km to the southwest of the Mongolian capital of Ulaanbaatar (Figure 1.2a). Most of the park is in Altanbulag *sum*, with northern edges in the Argalant and Bayanhangai *sum*s. The elevation of the park where it borders the Tuul River in the southeast is 1100 m, and it rises to 1842 m in the more mountainous northern part of the park (King and Gurnell 2005). Lowland steppe plant communities are most widespread in Hustai, occurring in the dry foothills and rolling plains and are dominated by *Atremisia adamsii* and *Stipa krylovii* (Wallis de Vries et al. 1996, King and Gurnell 2005). The higher elevation slopes host upland steppe communities and mountain steppe communities (Wallis de Vries et al. 1996). Annual average precipitation in Hustai is ~225 mm and annual average temperature is 2°C (Usukhjargal and Bandi 2013).

Average temperatures in January range from -23.5 to -17.4°C and average July temperatures range from 16.5 to 22°C (Bandi and Dorjraa 2012).

The takhi reintroduction programme in Hustai was developed and executed by the Foundation Reserves Przewalski Horse (FRPH) (Bouman and Bouman 1994, Boyd and Bandi 2002, King 2002, Bandi and Dorjraa 2012). On June 5, 1992 the first 16 takhi, shipped from reserves in the Netherlands or from Askania Nova, were released into fenced acclimatisation pastures at Hustai (van Dierendonck et al. 1996, Boyd and Bandi 2002, Bandi and Dorjraa 2012). Most of the reintroduced individuals had not known each other prior to reintroduction (van Dierendonck et al. 1996). Each group of individuals (two family groups and a group of bachelors) were kept in 0.4 – 0.45 km^2 enclosures a minimum of four km apart, visually and acoustically separated from each other (van Dierendonck et al. 1996, King and Gurnell 2005). The initial groups were released from their enclosures in 1994 (van Dierendonck et al. 1996, Boyd and Bandi 2002). Between 1992 and 2000 a total of 84 takhi were brought from European reserves to Hustai in five shipments (Bandi and Dorjraa 2012). The population has continued to grow steadily and at the beginning of this study there were 318 individuals living in 33 family groups and varied bachelor groups (Usukhjargal 2014). Of the 318 takhi, 104 (35.9%) were mares (5 years or older), 41 (12.9%) were fillies, 88 (27.7%) were stallions, 49 (15.4%) were colts, and 36 (11.3%) were foals (both sexes) (Usukhjargal 2014).

In 2012, 30 family groups of over 260 individuals used only 40 – 50% of the park area. The majority of individuals (24-25 family groups) were concentrated in the 100 – 150 km^2 area around the Bayan Am springs at the centre of the park (Bandi and Dorjraa 2012). Conservative space use by reintroduced takhi has been observed not only at Hustai, but also at GGB, and to an extent at Seer (Kaczensky et al. 2011, Bandi and Dorjraa 2012). This is probably partly due to the dependence of takhi on daily access to open water (Kaczensky et al. 2008, Bandi and Dorjraa 2012) but may also be due to home range fidelity. Takhi at all three reintroduction project sites were released into areas with immediate access to open water (Bandi and Dorjraa 2012). At Hustai, the first family groups were kept in enclosures in Bayan Am that allowed access to the Bayan Am spring (van Dierendonck et al. 1996). Once released from their enclosures they remained close by, only gradually moving away and expanding their range (King and Gurnell 2005).

Hustai family groups generally travel to water twice a day, particularly in the summer (King 2002). Most grazing occurs in the morning and evening, before and after the trek to water (van Dierendonck et al. 1996, King 2002). In the summer, late spring, and early autumn groups usually move up to higher elevations to rest during the heat of the day, generally seeking the shelter of woodland or rocky outcrops to avoid sun and biting insects (King 2002). In the winter, families prefer to rest on sunny south facing slopes, and frequently spend more time at lower elevations and in more sheltered areas than they do in warmer weather (King 2002).

1.5. Threats to the persistence of reintroduced takhi populations in Mongolia

The Mongolian takhi reintroduction efforts have been initially successful at all three locations, in that reintroduced individuals have survived and are reproducing. However, there remain many threats to the persistence of free-living takhi in Mongolia. The primary threats are extreme weather conditions, predation, disease, hybridisation risk, and interspecific resource competition.

1.5.1. Extreme weather events

The landlocked continental and arid climate of Mongolia lends itself to extreme variation in temperature and precipitation. High interannual variation, where temperatures range from -40 to 40^{o} C and summer drought and winter snowfall deep enough to make grazing impossible can easily occur within the same year, presents extreme risk to small and isolated animal populations such as those of reintroduced takhi. In the winters of 2000/2001 and 2009/2010 *zud* caused mortality rates of 21% and 60% respectively at GGB (Kaczensky et al. 2011). Hustai experienced losses of ~10% during each event (Usukhjargal and Bandi 2013), and the Seer population was not affected by the 2009/2010 *zud* (Association pour le cheval de Przewalski: TAKH 2013). Overall, the variation in the effect of the *zuds* in 2000/2001 and particularly in 2009/2010 on different reintroduction projects demonstrates how critical the establishment of multiple sub-populations will be to long-term survival of free-living takhi populations (Kaczensky et al. 2011).

1.5.2. Predation

The primary predators for wild equids in Asia are wolves (*Canis lupus*) and snow leopards (*Uncia uncia*) (Ransom et al. 2016). Other carnivores present at takhi reintroduction sites include red fox (*Vulpes vulpes*), corsac fox (*Vulpes corsac*), and Eurasian lynx (*Lynx lynx*) (Bandi and Dorjraa 2012). Smaller carnivores, as well as domestic dogs (*Canis lupus familiaris*), may scavenge takhi carcasses but they are unlikely to contribute to takhi mortality. Wolves are the main potential predator for Mongolian takhi. Both Hustai and GGB have reported high levels of wolf predation, particularly on foals (van Duyne et al. 2009, Bandi and Dorjraa 2012, Usukhjargal 2014) but some of the takhi listed as predated by wolves may have had another primary cause of death, such as disease or accident (Robert et al. 2005, van Duyne et al. 2009, Bandi and Dorjraa 2012). A study of wolf diet in Hustai using scat analysis found that across the three-year study period, takhi made up <1% of wolf diet, while livestock contributed to 63% of diet and red deer (*Cervus elaphus*) to 28% (van Duyne et al. 2009). To date, there have been no confirmed mortalities due to wolf predation at Seer, although attacks have occurred (Association pour le cheval de Przewalski: TAKH 2007).

1.5.3. Disease

The diseases that have caused the most deaths at the three takhi reintroduction sites are equine piroplasmosis (Babesiosis), strangles, and anthrax (although not confirmed as the cause for all suspected deaths) (King 2002, King and Gurnell 2005, Robert et al. 2005, Bandi and Dorjraa 2012, Feh 2014, Usukhjargal 2014). All three diseases were spread to reintroduced takhi populations through direct or indirect contact with domestic horses and other livestock (King 2002, Robert et al. 2005, Feh 2014). Thus, disease transmission is one risk that domestic horses pose to takhi in Mongolia.

1.5.4. Hybrids

Another risk posed by domestic horses is the dilution of takhi genetics through hybridisation. There are now over three million domestic horses living in Mongolia (Mongolian Statistical Information Service 2016), the majority of which often roam widely with minimal human interference (Joly et al. 2013). The ratio by which domestic horses outnumber takhi makes hybridisation a serious concern (Cordingley et al. 2009). The importance of domestic horses to Mongolian culture (Bold 2012) makes it unlikely that domestic horse populations will decrease in the short term. If hybridisation begins to occur between domestic horses and takhi at a high rate, it is unlikely that takhi can persist in the wild in Mongolia as a subspecies distinct from the domestic horse (Ryder 1993, Boyd and Houpt 1994). There are currently no official records of takhi/domestic horse hybrids in Mongolia, although hybridisation occurrences have been reported (Smith 2010 in Kaczensky et al. 2016). In 2014, 73 stallions at Hustai were bachelors while only 31 were family stallions (Usukhjargal 2014). A high number of competing stallions within the park will likely increase the number of bachelors moving outside the park to look for mares and could increase the number of fillies dispersing outside the park to avoid male harassment, which could increase hybridisation rates.

1.5.5. Resource competition

Competition with livestock for forage was considered one factor which contributed to takhi extinction in the wild in the 20th century (Bouman and Bouman 1994) and the overall number of livestock in Mongolia, including the number of domestic horses, has only increased since 1970 (Mongolian Statistical Information Service 2016). From 1970 to 2015 the number of domestic horses in Mongolia has increased from 2,312,001 to 3,295,336, while the number of sheep and goats increased from 17,518,406 to 48,536,049 (Mongolian Statistical Information Service 2016). Overgrazing of pasture and desertification have become an increasing concern in Mongolia, particularly in the south of the country (Hilker et al. 2014). A steady increase in the number of herbivores in combination with a decrease in available pasture will increase the probability of resource competition between takhi, other wild herbivores, and livestock.

The reduction of livestock in areas where takhi occur has been recommended at all reintroduction sites (Association pour le cheval de Przewalski: TAKH 2013, Kaczensky et al. 2016, Burnik Sturm et al. 2017) but as livestock are the primary source of income for many Mongolians, any reduction in livestock numbers would have to be accompanied by the development of equally, if not more, lucrative forms of income (Wakefield et al. 2002, Association pour le cheval de Przewalski: TAKH 2013).

1.5.6. Mitigating threats to takhi management through an understanding of takhi social structure

Known threats to the persistence of reintroduced takhi populations can be mitigated through adaptive management based on an understanding of takhi social structure and of how each individual contributes to interindividual relationships that drive the resource and space use of social groups. Understanding takhi social structure is particularly important for managing threats associated with contact with domestic horses (disease spread, hybridisation, and resource competition) as both subspecies have the same basic social structure (Boyd et al. 2016).

1.6. Group living as an ecological quandary and how equid social structure adjusts in response

All equids are social and spend at least part of their lives living in groups, but the structure, duration, and cohesion of the social groups is subject to variation across species, populations, and sometimes across time (Rubenstein 1981, Boyd et al. 2016). The two main types of equid social structure are usually described as female defence polygyny (Type I social structure) and resource defence polygyny (Type II social structure) (Klingel 1974, 1975, Boyd et al. 2016), although Rubenstein (1994) argues that when equid social structure is considered from the perspective of mare resource needs and social choices as well as stallion, both forms of social structure represent methods of resource defence.

1.6.1. Group living as a complex ecological problem

Group living in animals represents a complex ecological problem for individual group members, who must base their decision on whether to remain in their group on constant calculation and recalculation of the personal costs and benefits accrued by remaining versus leaving (Krause and Ruxton 2002). Animal groups vary widely in their size, longevity, cohesion, and complexity, and definitions of what constitutes an animal group are also varied (Krause and Ruxton 2002). Feh et al. (2001) considered khulan (*Equus hemionus khulan*) to be in the same group when the group 'diameter was less than the distance between groups and members showed coordinated movements during observation.' Ozogány and Vicsek (2015) used a similar definition, considering takhi family groups within a larger herd as occurring when '[family] members keep closer to each other than the distance between [families].' Overall, a fundamental aspect of group living is maintaining a certain level of proximity across time and space (Krause and Ruxton 2002, Whitehead 2008a).

1.6.2. Benefits and costs of group living

The potential benefits gained by an individual through living in a group include reduced predation risk, improved foraging and mating opportunities, improved thermoregulation, and more efficient travel (Krause and Ruxton 2002).

The chance that any one individual will be targeted by a predator decreases as group size increases (Duncan and Vigne 1979, Wrona and Dixon 1991, Fels et al. 1995, Krause and Ruxton 2002). For both resource and predator detection, a greater number of individuals increases the pool of information available to any one individual (Magurran and Higham 1988, Roberts 1996, Krause and Ruxton 2002, Conradt and Roper 2003, Wittemyer et al. 2005). The chances of an individual selecting a mate with good genetics are improved when there are more conspecifics to choose from, assuming correct assessment and truthful display (Dugatkin 1992, Rubenstein 1994, Kokko 1997, Johnstone and Earn 1999, Krause and Ruxton 2002). Birds, mammals, and insects have all been observed to conserve heat and water by huddling together (Roverud and Chappell 1991, Hayes et al. 1992, Ancel et al. 1997, Klok and Chown 1999, Krause and Ruxton 2002), and large waterfowl are a classic example of how travelling in a group reduces the cost to the individual (Hummel 1983, Kshatriya and Blake 1992, Krause and Ruxton 2002).

Along with the benefits of grouping come many costs, which include increased competition with conspecifics for resources, pseudo-interference (smaller food shares per individual when foraging with conspecifics, resulting in an individual exploiting poorer quality resources than they would if alone), possible increased targeting by predators, and increased rate of disease and parasite transmission (Free et al. 1977, Rubenstein 1994, Chapman et al. 1995, Krause and Ruxton 2002). Mechanisms of cohesion maintain the cohesion of animal groups at a level that maximises the benefits of group living for most individuals while minimizing the costs (Krause and Ruxton 2002).

1.6.3. Maintaining group cohesion

Group cohesion results from the push and pull of the costs and benefits met by individuals living in larger societies (Rubenstein 1994, Wittemyer et al. 2005, Sundaresan et al. 2007, Conradt et al. 2009, Bousquet 2011, Abell et al. 2013). Every change of group activity risks the loss of group cohesion, as the change is unlikely to be of maximum benefit to every individual in the group (Conradt et al. 2009, Bousquet 2011). There has been considerable research investigating the period at which groups make the decision to shift from one activity to another (Meunier et al. 2006, Bourjade, Thierry, et al. 2009, Conradt et al. 2009, Ozogány and Vicsek 2015). Individuals with the greatest need to obtain a resource at a different location are usually those that initiate movement, and individuals with less need of the resource but a greater interest in maintaining the social group follow (Conradt et al. 2009, Bousquet 2011). Group fission occurs if the benefits of moving are not sufficient to outweigh the costs for some individuals, and the benefits of staying are not enough to outweigh the costs for others (Meunier et al. 2006, Conradt et al. 2009, Pyritz et al. 2013).

At the moment of fission, leaving the group potentially provides access to necessary resources (food, water, shelter), but also potentially increases risk of predation and a loss of the shared information available among conspecifics (Krause and Ruxton 2002, Conradt et al. 2009, Schoenecker et al. 2016). Remaining in the group may offer safety, information and assistance, but also the potential for competition and interspecific aggression (Rubenstein 1994, Chapman et al. 1995, Krause and Ruxton 2002, Fischhoff et al. 2009). Strategies for minimizing interspecific aggression include policing and familiarity (Frank 1996, Krause and Ruxton 2002). Policing can maintain group cohesion by preventing stronger selfish individuals from monopolizing resources and driving weaker individuals from the group (Frank 1996, Flack et al. 2006). Familiarity and long-term relationships can also promote group cohesion by reducing interindividual aggression and improving the probability of co-participation in cooperative behaviours such as predator inspection or foraging (Dugatkin and Alfieri 1991, Dugatkin and Wilson 1992, Vonhof et al. 2004, Harris et al. 2007).

1.6.4. Equid social structure

Much of equid social structure is driven by equid anatomy. Equids are hindgut fermenters, with an enlarged colon, a caecum, and a commensal microbial population capable of digesting a high cellulose diet (Schoenecker et al. 2016). They are thus adapted to consume large quantities of low quality forage (Schoenecker et al. 2016). In consequence, equids can survive on grasses with very low protein to fibre ratios, but must consume large quantities of food at a rapid rate (Schoenecker et al. 2016). Because of their digestive anatomy, the best predictor of equid habitat use is forage abundance (King and Gurnell 2005, Schoenecker et al. 2016).

To obtain sufficient nutrients, equids spend more than 50% of their daily time budgets grazing (takhi: 52.3%±3.01, feral horses: 62.9%±4.79, plains zebras [*Equus quagga*]: 54.3%±6.86, khulan: 53.2%) (King et al. 2016). Lactating domestic horse mares require twice the protein and energy of standard maintenance levels (National Research Council 1978 in Boyd 1991) and lactating takhi mares have been observed to have a significantly higher bite rate during grazing than other reproductive classes (King 2002). Thus, while sufficient foraging time is essential for all equids, it is even more important for pregnant and lactating mares (Boyd 1991, Rubenstein 1994, Nowzari et al. 2013, Schoenecker et al. 2016).

Takhi, feral horses, plains zebra, and mountain zebra (*Equus zebra*) all practise female defence polygyny, or Type I social structure (Klingel 1975). They live in long-term, stable, non-territorial family groups (sometimes referred to as 'harems' or 'bands') consisting of one (sometime more) mature stallions, several mares, and their juvenile offspring (Klingel 1975, Boyd et al. 2016). Both colts and fillies disperse from the family unit when they reach sexual maturity, usually between one and four years of age (Bandi and Dorjraa 2012, Boyd et al. 2016). Fillies generally move to another family group, while colts usually join a bachelor group until they have the opportunity to form their own family (Bandi and Dorjraa 2012, Boyd et al. 2016). Asiatic wild ass (*Equus hemionus*), kiang (*Equus kiang*), and Grevy's zebra (*Equus grevyi*) all practise resource defence polygyny, Type II social structure (Klingel 1975, Boyd et al. 2016). With this social structure, the most enduring bonds are those between a mare and her recent offspring (Feh et al. 2001, Boyd et al. 2016) and larger social groups are built on fission-fusion societies that change in size and composition over time and across space (Sundaresan et al. 2007, Rubenstein et al. 2015). During the breeding season, stallions defend resources such as pasture or water, excluding other stallions but allowing mares and juveniles access (Klingel 1998).

The formation of Type I or Type II social groups of different equid species appears to relate to habitat adaptation. Those adapted to more mesic conditions tend to form stable family groups and those adapted to more arid habitats tend to form impermanent groups of varying composition (Boyd et al. 2016). The need for mares to maximise feeding time and ensure access to water, particularly while pregnant or lactating, and the need for stallions to minimise energy output while maximizing access to mares, together form fundamental drivers determining whether the social structure is built around family groups or fission-fusion societies (Rubenstein 1981, 1994).

Rubenstein (1994) proposed that, in open grasslands with a fairly even distribution of resources, stable family groups in equids allow mares to spend more time foraging and less time defending themselves and their offspring. His studies found that mares with stallions that had higher interstallion dominance were able to spend an additional six minutes per hour grazing (Rubenstein 1994), Mares with more dominant stallions also had more freedom of movement than the mares with less dominant stallions or mares on their own (Rubenstein 1994, Linklater et al. 1999).

1.6.4.1. Mare management of social structure

Mares can maintain a cohesive group structure in the absence of a stallion (Rubenstein 1994, Berger 1999). One feral horse family group whose stallion died unexpectedly remained together and successfully and repeatedly repelled the advances of young bachelors. They eventually allowed an older, previously dominant stallion to join them (Rubenstein 1994).

Mares will actively work together to prevent a new mare from joining a family group (Rubenstein 1994, Linklater et al. 1999). Thus, moving to a new group can be costly, while staying in a stable family group reduces exposure to aggression through stability and familiarity (Rubenstein 1994, Linklater et al. 1999, Bourjade, des Roches, et al. 2009, King et al. 2016).

Sigurjonsdottir et al. (2003) found that in domestic horse herds without mature stallions, mares were more socially active than in studies where mature stallions were also present. Mares engaged in mutual grooming more frequently and with a greater number of preferred grooming partners than mares in natural family groups (Sigurjónsdóttir et al. 2003). Further, their preferred partners were mares of similar age and rank, rather than their own subadult offspring, as is seen in family groups (Feist and McCullough 1976, Fischhoff et al. 2007). The juveniles instead spent a greater amount of time associating with geldings and peers (Sigurjónsdóttir et al. 2003). Mares also displayed stallion behaviours, including mounting other individuals and protecting foals from conspecifics (Sigurjónsdóttir et al. 2003) something also seen in other mare-only groups (Berger 1999).

Mares, geldings, and juveniles of both sexes have been observed to intervene in affiliative interactions involving a preferred social partner, regardless of whether their group included stallions (van Dierendonck et al. 2009, Schneider and Krueger 2012). The authors have suggested that these interventions are a way for individuals to safeguard their position within their social network, by preventing preferred partners from forming other strong social bonds (van Dierendonck et al. 2009, Schneider and Krueger 2012).

The additional affiliative and interceptive interactions observed by Sigurjonsdottir et al. (2003), van Dierendonck et al. (2009), and Schneider and Krueger (2012) may represent an alternative strategy for reducing intergroup conflict and competition. Perhaps when Type I species form larger, more loosely structured groups, where multiple social partners are available and stallions aren't actively maintaining family group borders, it is beneficial for mares to actively and pre-emptively manage established social bonds.

1.6.4.2. Stallion management of social structure

Takhi, feral horse, and plains zebra stallions tend to spend more time moving and less time feeding than do the mares in their family groups, although this difference in time budget by sex has not been observed in all plains zebra populations or in Camargue horses (Rubenstein 1986, Boyd 1991, King 2002, Rubenstein and Hack 2004, King et al. 2016). Takhi stallions change behavioural state on average 66±4 times per hour, while mares only change state 55±3 times per hour (Boyd 1991). In keeping with this trend, stallions displaying typical family-tending behaviour generally show less synchronous behaviour than the rest of the group (Boyd and Bandi 2002, Souris et al. 2007). In this way, the behaviour of family stallions (or some mares, particularly in groups without stallion) is similar to the policing role described by Franks (1996) and Flack (2006). By investing extra energy to minimise conflict and harassment, stallions increase their attractiveness as potential consorts (Rubenstein 1994). The investment of time and energy in maintaining a family group is repaid by giving the family stallion greater and more frequent access to mares and thus increasing his potential reproductive success rate. Paternity tests of feral horse populations have found that family stallions sire 85-86% of their family's foals (Feh 1990, Kaseda and Khalil 1996, King et al. 2016).

Some stallions, who may not be capable of maintaining their own family group, will instead form an alliance with another stallion (Feh 1999, Boyd et al. 2016). Feral and semi-feral horses (Feh 1999, Linklater et al. 1999), takhi (Bandi and Dorjraa 2012), and plains zebra (Klingel 1967 in Boyd et al. 2016) have all been observed to form multi-stallion families. From the perspective of the individual stallion, a multi-stallion group does not yield greater reproductive success than a single stallion group, but stallion alliances do make lower ranking individuals better able to defend their mutual family group from other stallions (Feh 1999), improving their attractiveness as consorts to mares. Feh (1999) reported higher foal survival in multi-stallion families than in single stallion families, although Linklater (1999) found higher survival in foals from single-stallion families and also better overall body condition in the mares. It may be that the relationship between the stallions dictates how disruptive a multi-stallion family structure is to the mares.

1.6.4.3. The influence of resource availability on equid social structure

Equid family group cohesion is less strong when resources are scarce. Type II social structure appears where patchy foraging makes the costs of competition between group members greater than the benefits of membership in a group (Rubenstein 1994). For arid adapted species, the differing water requirements for lactating and non-lactating mares also contribute to the fission-fusion nature of their social structure (Becker and Ginsberg 1990, Rubenstein 1994, Sundaresan et al. 2007, Nowzari et al. 2013), especially in areas where the best grazing sites are a long distance from water sources (Rubenstein 1989). The need of lactating mares for regular access to water can even cause the social cohesion of mesic-adapted Type I species to break down in extreme habitat and weather conditions (Rubenstein 1981, 1994).

Variation has also been found in the level of impermanence of Type II social groups. A comparison of the social structure of Grevy's zebra and onagers (*E. hemionus onager*) found that Grevy's zebra societies were formed of cliques of mares (usually of the same reproductive state) who continued to associate over time and stallions who showed no preference for particular associates (Sundaresan et al. 2007, Rubenstein et al. 2015). Lactating mares were more likely to switch communities than non-lactating mares, probably because of their need for higher quality resources over time (Rubenstein et al. 2015). Onagers of all reproductive classes and both sexes did not have long term consistent associates (Sundaresan et al. 2007, Rubenstein et al. 2015). Rubenstein et al. (2015) hypothesized that formation of longer term relationships in Grevy's zebra was due to predation pressure, which was not a factor for onagers. By remaining in social cliques, Grevy's zebras reduced the risk of finding themselves alone on the landscape in the presence of predators (Rubenstein et al. 2015).

1.6.4.4. Drivers of equid social structure

Overall, the social cohesion and structure of equid groups appears to be directly related to balancing the costs and benefits of remaining in a group. For arid-adapted species, necessary resources are more challenging to acquire and the difference in resource requirements for different members leads to a more variable series of associations. For mesic-adapted species, the social benefits of a stable group usually outweigh the costs of balancing individual needs against the needs of the rest of the group. Thus, the social cohesion of equid groups runs along a spectrum related to the relative strengths of ecological and social pressures, both of which are related to sex and reproductive state. Mare reproductive success is limited by access to resources, while stallion success is limited by access to mares (Rubenstein 1994). Therefore, mares tend to control resource-based group movements and, ultimately, the decrease or increase of social cohesion, while stallions, within the constraints exerted by mares, tend to control socially based movements (Rubenstein 1994).

1.7. Variation in takhi cohesion at the herd level

To date, reintroduced takhi have only been observed to display Type I social structure (Boyd 1991, King 2002, Kaczensky et al. 2008, Bourjade, des Roches, et al. 2009). Mean family size is usually eight individuals but ranges from two to 22, usually with two to four adult mares (Boyd et al. 2016). The family group units show a fission-fusion style variation in structure at the herd level. Individual families sometimes travel alone and independent of other family groups, sometimes form larger impermanent herds at shared resources such as water or good pasture, and sometimes travel together in larger herds which may consist only of family groups or also include bachelor groups on the fringes (Bandi and Dorjraa 2012, Ozogány and Vicsek 2015, Boyd et al. 2016).

Of the three reintroduction locations in Mongolia, the takhi herds at Hustai are the most impermanent, usually only forming temporarily at water sources. Sometimes multiple family groups will move to the same hillside to graze and rest, but with no indication that they are actively travelling together. Studies of family group home range and spatial use between 1996 and 2000 at Hustai found that six families (and four additional families in 1999 and 2000) had a mean home range overlap of 39%, ranging from 0% to 89% (King and Gurnell 2005). The families initially established home ranges in valleys not occupied by other families (King and Gurnell 2005). Throughout the study, multiple families were observed resting or grazing in the same valley (King and Gurnell 2005). Later studies of family home range at Hustai also found different families had overlapping home ranges, primarily in the valley in which the first groups were originally released (King and Gurnell 2005, Nandintsetseg 2008).

In GGB family groups and bachelor groups have been observed to form larger herds with up to five family stallions and 70 individuals (Kaczensky et al. 2008, Bandi and Dorjraa 2012). These larger herds were observed from 2005 to 2010 and persisted through multiple seasons (Bandi and Dorjraa 2012).

The three main families at Seer travel, graze, and rest together in a loosely cohesive herd. Occasionally, one family will travel independently for one to several days and then rejoin the other groups. During the study period an older mare and several dispersing juveniles of both sexes formed a fourth group, which did not travel with the family groups and was often driven away from the herd by the family stallions.

The family and bachelor groups of takhi living in the semi-reserve in Hortobágy National Park form a cohesive herd of 240 individuals (Ozogány and Vicsek 2015). The family groups are stable in membership, while the bachelor groups rearrange more frequently (Ozogány and Vicsek 2015). The herd structure was not initially observed at Hortobágy, and it is not known whether the shift to herd structure was based on increased interindividual familiarity or increased population density in an enclosed area (Ferdinandy et al. 2017).

Plains zebra also form large, loosely connected herds of cohesive family groups (Fischhoff et al. 2007, Tong et al. 2015). These herds appear to form as a result of reproductive mares, family stallions, and bachelors all balancing needs to obtain sufficient forage, avoid predation, and maximise reproductive success (Rubenstein and Hack 2004). Preferential associations were observed to form between pairs of families, but above the level of these preferential associations herds formed of anywhere from two to 100 families (Rubenstein and Hack 2004). Rubenstein and Hack (2004) argued that for mares, there is no significant difference in competition when grazing in a herd versus grazing in a solitary family group. For stallions, travelling and grazing with other families increases the chance of conflict between family stallions, but also decreases the number of bachelor/family stallion interactions each individual family stallion must engage in, which increases individual foraging time and reduces energy expended in socialising (Rubenstein and Hack 2004).

Feral horse groups in Wyoming, in the US, did not form herds, but did have clearly defined hierarchies that determined the sequence of access to limited water sources (Miller and Denniston 1979). Families appeared to recognise both the identity and hierarchical positions of other families approaching the water source, and would stop drinking and move away at the approach of a higher-ranking group (Miller and Denniston 1979).

Reports of takhi social structure prior to their extinction in the wild described families of 15 to 20 individuals that would occasionally unite in larger herds of over 100 (Dagva 1954 in Klimov 1988). Thus, the variation in herd cohesion observed at the reintroduction sites may represent another tier of social structure in takhi above the family group which was unobservable in the artificial social groups of captive individuals prior to release.

1.8. Behavioural mechanisms of cohesion and the role of interactions

Although there are many studies investigating when and where social groups form, and when and why groups separate, there has been limited research into what behavioural mechanisms maintain group cohesion.

The best surrogate metric for group cohesion is interindividual distance, as a lack of group cohesion is, by definition, individuals changing behaviour state and moving apart until they are no longer in the same group (Meunier et al. 2006, Conradt et al. 2009). Measuring interindividual distance in large wild animals without disrupting the spatial distributions being measured is challenging, and most studies to date have only used rough estimates of spatial distribution, such as body length units or nearest neighbours (Linklater et al. 1999, Clutton-Brock et al., 1982 in Croft et al. 2008, Bousquet 2011). An individual's position within a group is important because it influences immediate individual fitness (Bousquet 2011). For example, banded killifish (*Fundulus diaphanous*) increase interindividual distance when they are hungry, and decrease distance (increasing cohesion) when they are alarmed (Hoare et al. 2004).

Behavioural mechanisms of social cohesion are behaviours that influence interindividual distance and, by extension, group cohesion (Krause and Ruxton 2002). Behavioural mechanism research to date has primarily focused on species other than mammals. Examples include; identification of a pre-flight signalling mechanism in swans (Black 1988), spatial interaction rules shaping group cohesion in fish (Hoare et al. 2004), and cooperative 'drumming' signals as a mechanism for cohesion in sawfly larvae (Fletcher 2008). Cozzi et al. (2010) suggested that domestic horses may use affiliative interactions as a mechanism for maintaining group cohesion following conflict.

Individual spatial proximity and overall group distribution are closely tied to interindividual interactions. Proximity in horses can be a component of affiliative or agonistic behaviour (van Dierendonck et al. 2009) and interindividual interactions between animals are important indicators of social rules and structure (Hinde 1976, Lehner 1996). Interindividual interactions, when the action of one animal is directed toward another or affects the behaviour of another (Whitehead 2008a), have a visible influence on the spatial distribution of individuals and the maintenance of group cohesion through the push and pull of agonistic and affiliative social exchanges (Hoare et al. 2004, Ballerini et al. 2008, Cozzi et al. 2010).

1.8.1. Affiliative interactions

Affiliative interactions are those that promote social bonds and increased spatial cohesion. The primary affiliative interactions displayed by equids are mutual grooming and play (van Dierendonck et al. 2009). Both have been found to be important for the welfare of domestic horses (van Dierendonck and Spruijt 2012).

Mutual grooming (or allogrooming) occurs between and among individuals of all age and sex classes (Sigurjónsdóttir et al. 2003, van Dierendonck et al. 2004, Bourjade, Tatin, et al. 2009, van Dierendonck et al. 2009). During grooming bouts, individual horses typically stand parallel to each other, facing opposite directions (Feh and de Mazieres 1993, King 2002). They use their lips and teeth to rub and scratch the neck, withers, and rump of their grooming partner (Feh and de Mazieres 1993). Mutual grooming has the practical benefit of removing parasites and shedding hair from difficult to reach areas (King 2002, King et al. 2016) but it also has important social and psychological benefits (Feh and de Mazieres 1993, van Dierendonck and Spruijt 2012). Mutual grooming has been demonstrated to reduce the heart rate of participators (Feh and de Mazieres 1993) and to occur at a greater frequency in newly formed social groups than in more established groups (Feh and Carton de Grammont 1995 in King

2002). Feh (1999) identified mutual grooming as one interaction by which alliance stallions maintained their cooperative relationship. Grooming is almost always reciprocated (hence 'mutual') and is only observed between individuals who are familiar with each other (Wells and Goldschmidt-Rothschild 1979, Sigurjónsdóttir et al. 2003, Fischhoff et al. 2007, King et al. 2016). Individuals tend to have preferred grooming partners, but grooming partnerships are not exclusive (Wells and Goldschmidt-Rothschild 1979, Crowell-Davis et al. 1986, Boyd 1988a, Keiper and Receveur 1992, King et al. 2016). It therefore follows that mutual grooming patterns can provide important insight into the structure of equid social groups.

Play is seen most frequently in males, particularly colts (Sigurjónsdóttir et al. 2003, van Dierendonck et al. 2009, Bourjade, Tatin, et al. 2009). Mares participate only rarely (Sigurjónsdóttir et al. 2003). Foals begin to play alone when they are two days old, and start to play with other conspecifics in their third week (Boyd 1988a). Play is energetically costly, which is one reason it is primarily seen more in young individuals and equids living in more mesic environments (Moehlman 1998, McDonnell and Poulin 2002, King et al. 2016). Play aids the development of motor, social, and cognitive skills (Khalil and Kaseda 1998, Cameron et al. 2008, van Dierendonck and Spruijt 2012) and is also important for building social relationships (Feh 1988). Play can also be a way for individuals to settle minor dominance questions without resorting to aggression (Goodwin and Hughes 2005).

Other affiliative interactions listed in studies include progressive steps in the process of initiating contact with another conspecific, such as 'approach', 'olfactory investigation', and other forms of body contact, (Christensen et al. 2002, Bourjade, des Roches, et al. 2009, Cozzi et al. 2010). Proximity, and maintenance of proximity, has also been described as an affiliative behaviour (van Dierendonck et al. 1995, 2004).

1.8.2. Agonistic interactions

Agonistic interactions are those that promote increased distance between individuals (Feh 1988). They are often also described as aggressive or defensive behaviours (Feh 1988, Rubenstein 1994, Bourjade, des Roches, et al. 2009, Cozzi et al. 2010) and are usually the interactions used to settle questions of dominance (Miller and Denniston 1979, Feh 1999). Basic agonistic interactions include head threats, bite threats, bites, charging, chasing, kick threats, and kicking (Feh 1988, Rubenstein 1994, Christensen et al. 2002, Bourjade, des Roches, et al. 2009, Cozzi et al. 2010). Head, bite, and kick threats are the mildest agonistic interactions and occur the most frequently (Feh 1988, Keiper and Receveur 1992). They are often used to assert dominance or maintain personal space or access to resources (Feist and

McCullough 1976, Feh 1988, King 2002, Bourjade, Tatin, et al. 2009). Charging and chasing are more aggressive and offensive interactions (van Dierendonck et al. 1995).

Kicks and also kick threats can be used offensively or defensively (Feh 1988, van Dierendonck et al. 1995, King 2002). In contrast, charging, chasing, head threats, and bite threats are unambiguously offensive and agonistic interactions (Feh 1988, van Dierendonck et al. 1995, King et al. 2016).

1.8.3. Other interactions

There are also interactions that are neither affiliative nor agonistic in their effect on spatial distribution. Two very visible interactions with an ambiguous effect on interindividual distance are snapping and herding.

Snapping (also referred to as 'clapping') is a submissive opening and closing of the mouth used by juvenile horses and takhi to deflect aggression (Christensen et al. 2002). Juveniles will snap while retreating from an aggressor but will also snap while approaching a dominant individual or when frightened by an interaction between two other conspecifics (Houpt and Boyd 1994). In donkey and zebra species only, snapping is also seen in fillies and mares in oestrous (Houpt and Boyd 1994).

Herding is a behaviour typified by pinned ears and a lowered head and is used by stallions to direct the movement of the family group (King 2002, King et al. 2016). It can technically be either agonistic or affiliative, as the purpose can be to move one or several group member(s) away from or toward conspecifics or simply to assert dominance (King et al. 2016).

1.9. Individual variation and its influence on social cohesion

The most basic building blocks of social structure are the interactions that occur between individuals (Hinde 1976). However, the individuals themselves can show considerable variation in age, sex, personality, and personal history (Whitehead 2008a) and this variation can strongly influence the type and frequency of interactions that occur, and thus the structure of the society overall (Whitehead 2008a).

Differences in the age, sex, and reproductive state of members of a social group often have a strong influence on an individual's position within the group's social structure. Social roles, or at least tendencies, based on reproductive state have been described in most taxa, from obligate eusocial insects to humans. Equids are no exception, as has been discussed in section 1.6.4. The social roles of individuals of differing reproductive state can in turn influence an individual's contribution to the social cohesion of the group. Flack et al. (2006) found that the removal of adult males from a pigtailed macaque (*Maca nemestrina*) population resulted in the destabilization and break down of a larger social group into smaller and less diverse cliques. Fedurek and Lehmann (2017) found that subadult olive baboons (*Papio anubis*) contributed to the cohesion of their social group by providing a social bridge between adults and juveniles.

Variation in the relationship of an individual with other members of the social group can also have a strong influence on social cohesion. Yearling female yellow-bellied marmots (*Marmota flaviventris*) promote social cohesion through high rates of affiliative interaction, and tend to interact most with other individuals of the same age or to whom they are related (Wey and Blumstein 2010). Tong et al. (2015) found that plains zebra females who were members of the same herd were more closely related than would be expected by chance. Thus, variation in relatedness has also been found to influence social cohesion.

Equids appear to use familiarity as a surrogate for relatedness, and multiple studies have proposed familiarity as the mechanism by which inbreeding is avoided (Duncan et al. 1984, Berger and Cunningham 1987, Monard et al. 1996). Dispersing juveniles of both sexes appear to avoid mating with members of their natal group, whether or not they are actually related (Duncan et al. 1984, Berger and Cunningham 1987, Monard et al. 1996). Feh (1999) found that mares and stallions separated for one year would reform their family group, even with many other individuals present. Berger (1986) found that stallions played significantly more with familiar colts. Thus, familiarity could have a strong influence on social cohesion, as familiarity promotes tolerance of proximity, particularly of adults for familiar juveniles. Berger (1986) found that after two years of separation stallions would attempt to mate with their daughters and fight with their sons, so social restrictions based on familiarity appear to have at time limit.

Variation in individual personality has also been shown to influence structure and cohesion in animal social groups. Sibbald et al. (2009) found that artificially formed groups of shy sheep were more cohesive than groups of bold sheep. Yearling female marmots who were more social in their natal groups were less likely to disperse than those that were less social (Blumstein et al. 2009). Aplin et al. (2013) found that slow-exploring great tits (*Parus major*) formed more stable relationships, while fast-exploring individuals formed less stable relationships but with a greater number of individuals. Personality has been observed to potentially influence intragroup cohesion in takhi populations, with more assertive takhi tending to be found at the edge of family groups, and more social takhi tending to move at the centre of the group (Baker 2015).

Thus, individuals of differing reproductive state, personality type, or relative familiarity and relatedness may occupy significantly different positions in the social structure of takhi family groups and herds.

1.10. Factors expected to influence social cohesion in takhi

From review of the literature, it appears that the key factors influencing group cohesion in studied equid populations can for the most part be broken down into female priorities and male priorities. To be successful in a biological sense (survival and reproduction), females require constant access to food, access to water, and minimised risk of intraspecific harassment (Rubenstein 1994, Nowzari et al. 2013, Schoenecker et al. 2016). For males to be successful, they require access to females and minimised risk of costly confrontations (Berger 1986, Rubenstein 1994). For Type I equids such as takhi, a social structure based on the formation of relatively stable family groups best meets the requirements of both sexes.

Reasons for variation in intergroup cohesion resulting in the formation, or lack of formation, of herds is more challenging to explain. Proposed explanations include relatedness of females (Tong et al. 2015), shared risk of confrontation with bachelors (Rubenstein and Hack 2004), and diffusion of predation risk (Rubenstein and Hack 2004, Rubenstein et al. 2015).

Cohesive herds of takhi have been observed to persist in populations with little to no predation (Seer and Hortobágy) and limited pressure from bachelors (Seer). Herd formation in populations where external pressures observed elsewhere do not occur suggests that intragroup and intraherd relationships may be the drivers of both intra- and intergroup cohesion. Intra- and intergroup social structure is formed from social ties existing between many pairs of individuals. It may be that the key to variations in cohesion can be found in the characteristics of the individuals who make up the social groups. From the literature, the individual characteristics most likely to influence group cohesion are reproductive state, personality type, and interindividual relationships defined by familiarity, relatedness, and interindividual proximity and social interactions.

1.11. The applicability of social network analysis for investigating social cohesion

Animal social network analysis is a rapidly developing field that has been used for investigating the social structure of species ranging from dolphins (Lusseau and Newman 2004), to guppies (Croft et al. 2006), to lions (Abell et al. 2013), to other equids such as zebra and onager (Sundaresan et al. 2007, Rubenstein et al. 2015). Social network analysis can be used to describe the social organization of groups of individuals at the dyadic, group, and herd level based on many different association types, including spatial distribution and interindividual interaction rate (Whitehead 2008a). Thus, it is an ideal method for exploring the relationship between individual characteristics, interindividual relationships, and overall social structure. Social network analysis is most powerful when it is used to analyse the structure of a closed population where all individuals are known and easily identified (Croft et al. 2008), which makes the reintroduced takhi populations at Hustai, and particularly those at Seer, ideal candidates for this method of analysis.

1.12. Thesis aim and structure

The overall aim of this thesis is to investigate possible behavioural mechanisms of intragroup and intergroup social cohesion in takhi family groups. An understanding of the factors influencing the presence or absence of cohesion at the group and herd level in reintroduced takhi populations will aid in the development of adaptive management strategies and the mitigation of known threats to the persistence of takhi in Mongolia, particularly threats related to habitat use, resource requirements, and contact with domestic horses. The thesis focuses on individual variation as a potential source of observed variation in social cohesion.

The thesis is divided into seven chapters. The first chapter has provided background for the overall thesis. It briefly describes the history of takhi conservation and reintroduction programmes, discusses research into the proximate and ultimate drivers of group formation in animals, provides a review of our current understanding of the structure and variation of equid societies, and outlines possible sources of observed variation in equid social structure.

The objective of Chapter 2 is to determine whether it is possible to identify repeatable personality traits in takhi. The chapter provides a review of equid personality research and develops and applies methodology for assessing personality in free-living takhi. The results of the personality assessments conducted in this chapter are applied to the social network analyses in later chapters.

The objective of Chapter 3 is to determine and describe the best animal social network analysis methods for application in the social network analysis research chapters. Chapter 3 includes a general overview of social network analysis theory and terminology. The chapter also describes the methodology applied in the following three social network analysis research chapters.

Chapters 4, 5, and 6 are social network analysis research chapters. All three chapters investigate the potential influence of individual characteristics on interindividual relationships occurring both within family groups and between members of different family groups, with the aim of identifying individuals with the greatest influence on intragroup and intergroup social cohesion. Each chapter explores a separate category of interindividual relationship. All chapters look at the importance and centrality of individuals in spatial and interaction networks relative to their reproductive state, group membership, and personality. The objective of Chapter 4 is to investigate whether an adult takhi's group, personality, or reproductive state is related to its importance in adult peer networks. The objective of Chapter 5 is to determine whether a juvenile takhi's group, personality, or sex is related to its importance in juvenile peer networks. The objective of Chapter 6 is to determine whether adult/juvenile relationships are influenced by individual group membership, reproductive state, or personality.

Chapter 7 presents a discussion of the general findings of the four research chapters and the resulting broader picture of takhi social structure. The chapter discusses how the results of the study can inform the management strategies of takhi reintroduction projects in Mongolia, as well as other equid populations with similar social structure. Finally, the chapter also discusses the limitations of the study and suggests avenues of further research.

2. Assessing personality traits of free-living takhi in a natural social setting

2.1. Introduction

The importance of the individual to overall population structure and dynamics has become increasingly acknowledged in the literature in recent decades (Dingemanse and Reale 2005, Reale et al. 2007). Effects of individual influence can clearly be seen from studies of the influence of individual personality on dispersal and reproductive success (Dingemanse and Reale 2005, Pruitt et al. 2008, Cote et al. 2010), reintroduction success (Banks et al. 2002, Bremner-Harrison et al. 2004), and group social structure (Aplin et al. 2013, Wolf and Krause 2014). Personality assessment can be valuable in informing management decisions, but is often labour intensive and logistically challenging to conduct, particularly when working with animals in the field, and particularly when working with large, social species.

With ~2000 individuals in existence, and wild populations ranging in size from 400 to as small as 50, every individual takhi has a high potential influence on overall population structure, both genetically and socially, and locally and globally. Takhi family group structure generally remains stable over time, and mare reproductive success is limited by access to resources, while stallion success is limited by access to mares (Chapter 1, section 1.6.4, Rubenstein 1994). Therefore, mares tend to control resource based group movements, and stallions tend to control socially based movements (Rubenstein 1994). In this dynamic social structure, the needs of each individual contribute to the overall behaviour of the group. From a management perspective, an understanding of how individual takhi vary in their behaviour, and how that behaviour can be reliably assessed, becomes a valuable tool. The interactions of individuals, particularly in a social species such as takhi, form the foundation of a species' social structure. Social structure in turn shapes patterns of mortality, reproduction, and dispersal (Whitehead 2008a).

2.1.1. Defining animal personality

'Animal personality' is now generally accepted to mean observed differences in the behaviour of individuals that are consistent over time and across situations (Gosling 2001, Reale et al. 2007). Behaviours are consistent not in the sense that they remain fixed, because responses may change with age, group composition, or environment, but in sense that the relative response of each individual compared to its conspecifics remains consistent.

The scientific community has now accepted animal personality as a definable and relevant aspect of ethological, biological, and ecological research (Bekoff 1977, Gosling and John 1999, Gosling 2001, McDougall et al. 2006, Reale et al. 2007, Sih and Bell 2008). Although the importance of the individual as a variant of type on which natural selection can act has long been acknowledged (Darwin 1859), for years individual variation in behaviour was considered to be anthropomorphic projection or background noise to be compensated for or ignored (Reale et al. 2007). More recently, variation among individuals has come to be considered as an adaptive and plastic product as much as, or more than, a means unto an evolved end (Reale et al. 2007). Multiple studies have now found conclusive evidence that individual behavioural variation influences important processes including dispersal (Dingemanse et al. 2003, Bremner-Harrison et al. 2004, Blumstein et al. 2009), resource acquisition (Sibbald et al. 2009), mate choice (Dingemanse and Reale 2005), offspring recruitment (Dingemanse and Reale 2005, Duckworth and Badyaev 2007), and social interactions (Aplin et al. 2013, Wolf and Krause 2014, Briard et al. 2015). Recent developments with social network analysis have demonstrated how interindividual interactions can vary in type and frequency depending on individual characteristics, including personality, and the overall structure of communities and populations (Aplin et al. 2013).

2.1.2. Common methods of personality assessment

To assess personality in individuals, it is necessary to be able to detect variation, repeatability, and, ideally, heritability in individual traits (Reale et al. 2007). A personality trait shows variability if there is an observable difference in behaviour frequency or response between individuals (Reale et al. 2007). A trait shows repeatability if there is a consistent trend in individual behaviour frequency or response across time or situations (Bell et al. 2009). A trait shows heritability if there is a consistent similarity in individual behaviour frequency or response between parent and offspring (Duckworth and Badyaev 2007, Reale et al. 2007). Traits are only expected to be partially heritable (van Oers et al. 2005), but they must be variable and repeatable to be considered personality traits (Reale et al. 2007). Three different methods are commonly used to assess personality traits; observer rating, ethological coding (also known as observer assessment, observer coding, or naturalistic observation), and experimental assessment (Smith and Blumstein 2008, Highfill et al. 2010, Bremner-Harrison et al. 2017).

2.1.2.1. Observer rating

Observer rating uses a human observer as an intermediary assessor of animal personality. After observing the focal animal for a short or extended period of time (up to several years), the observer is asked to assess how much the focal animal displays certain character traits or certain behaviours, typically using a series of adjectives accompanied by a Likert or visual analogue scale (Lloyd et al. 2007, Williams 2013) or some similar metric. The observer rating method was initially accompanied by concerns that anthropomorphising would influence results, but comparisons between rating and coding methods have shown that with clearly defined questionnaires, rater results show high repeatability and significant agreement with other assessment methods (Le Scolan et al. 1997, Gosling 2001, Lloyd et al. 2007), although it is best for the raters to be familiar with the species generally and to all have interacted with the animals in similar circumstances (Highfill et al. 2010, Watters and Powell 2012).

2.1.2.2. Ethological coding

Ethological coding uses standard ethological methods, usually either focal animal continuous or scan sampling (Altmann 1974, Watters and Powell 2012) to record observed behaviour frequencies over time. It is the most objective and hands-off method of assessment and can be used with animals that cannot be isolated from their peers or handled, but does require a significant time investment. The behaviours that are considered relevant during observation will vary depending on the personality trait(s) being assessed.

2.1.2.3. Observer rating vs ethological coding

Ethological coding is a much more labour-intensive method than rating, but it may be less likely to introduce error from interpretation. Rating can yield a large dataset with relatively little additional effort from each rater, but is limited by the number of and the experience of observers available. Rating and coding can generate significantly similar results, and several researchers have advocated the use of both rating and coding as a means of comparison and verification when assessing animal personality (Gosling and Vazire 2002, Highfill et al. 2010, Watters and Powell 2012).

2.1.2.4. Experimental assessment

In an experimental situation, tests are conducted in a relatively controlled environment and usually targeted towards assessing a specific trait; for example, presenting an individual with a novel object in a familiar setting to test for boldness (Bremner-Harrison et al. 2004, Stratton 2015, Bremner-Harrison et al. 2017). Ideally, the test produces a reaction that varies between individuals, but does not cause a reaction so strong or weak that no variation between individuals can be detected (Reale et al. 2007). Individual reactions to the test can be recorded using either or both rating and coding (Highfill et al. 2010).

Depending on the species being assessed, experimental personality tests in a controlled environment may not be feasible. Takhi cannot be temporarily brought into captivity, or even captured, without very high cost, high risk, and extreme disruption to all members of the social group. Experimental manipulation in the field may be possible for species that are relatively solitary or dependent on spatially restricted resources, such as den sites and watering holes, that make it easier to minimise variation in the testing environment and the duration of observation for each individual (e.g. Bremner-Harrison et al. 2013). For animals that live in larger social groups such as takhi, it is difficult to ensure that all members receive the same exposure (in terms of duration and intensity) to the test situation and that the reaction of an individual is not influenced by other members of the social group (King, Williams, et al. 2015). For these reasons, experimental assessment methods were not applied for this study.

2.1.3. Previous research on equid personality

Assessments of equid personality to date have focused almost exclusively on domestic horses (Gosling 2001, Ito et al. 2015). Two studies were found which dealt with wild equid personality assessment. Ito et al. (2015) described variations in androgen receptors between domestic horses and three zebra species (Grevy's zebra, plains zebra, and mountain zebra) and discussed the possible link between the receptor gene and the relative aggressiveness of the species, but did not actually test variation in aggressiveness in individuals of different species. Baker (2015) used multiple methods to test for personality traits in takhi living semi-wild at Le Villaret nature reserve in southern France. Tilson et al. (1988) considered stallion personality, referred to as 'temperament' in the paper, to be a deciding factor in the success of attempts to form peaceful takhi bachelor groups in captivity, but did not offer a definition of 'temperament.' Berger (1977) used ethological coding to develop an 'index of nervousness' for individuals in families of feral horses based on their vigilance while drinking. No other studies of non-domestic equid personality were found in the literature.

The most common methods of personality assessment of domestic horses in the literature were observer rating and experimental assessment (Table 2.1). In a few studies ethological coding was used during standard work routines or non-manipulated in-stable or turn-out periods (Table 2.1, Seaman et al. 2002, Lloyd et al. 2007, Hausberger et al. 2011, Bulens et al. 2015, Lansade et al. 2016).

Table 2.1. Personality traits found in domestic horse personality research and the assessment methods used to extract them. * indicates factors obtained from PCA of ethological coding scores and experimental tests. Letters in parentheses describe the metric/method when experimental assessment was used. C = coded reactions, D = duration of targeted behaviours, I = distance travelled during test, F = frequency of targeted behaviours.

Authors	Personality traits	Assessment method	# horses
Anderson et al. (1999)	Many paired adjectives	NA	103
Bulens et al. (2015)	Reactivity	Experiment (C)	54
Hausberger et al. (2004)	Emotionality	Experiment (C)	702
Hausberger et al. (2011)	Excitability	Experiment (C)	119
Ijichi et al. (2013)	Agreeableness Neuroticism Extroversion Gregariousness towards people Gregariousness towards horses Proactivity* Human-horse relationship* Sociability* Threat Avoidance*	Observer rating Experiment (D/I)	146
Lansade and Simon (2010)	Fearfulness Gregariousness Activity level Reactivity to humans Sensory sensitivity	Experiment (C/D)	36
Lansade et al. (2008)	Sensory sensitivity	Experiment (C/D)	26
Lansade et al. (2008a)	Fearfulness	Experiment (C/D)	110
Lansade et al. (2008b)	Gregariousness	Experiment (C/D)	110
Lansade et al. (2016)	Reactivity to humans Tactile sensitivity Fearfulness Gregariousness Locomotor activity	Experiment (C/D)	24
Le Scolan et al. (1997)	Fearfulness Nervousness Gregariousness Learning abilities at work	Observer rating (verified with experiments) Experiment (C/D)	72
Lloyd et al. (2007, 2008)	Anxiousness Dominance Excitability Inquisitiveness Protection Sociability	Observer rating Ethological coding	61; 1223
McGrogan et al. (2008)	Agreeableness Extraversion Neuroticism	Observer rating	100
Morris et al. (2002, 2002)	Neuroticism	Observer rating	10

	Extraversion Openness Agreeableness Conscientiousness		
Seaman et al. (2002)	Activity/Passivity	Experiment (C/D) Ethological coding Observer rating	33
Valenchon et al. (2013)	Reactivity to humans Sensory sensitivity Fearfulness Gregariousness	Experiment (C/D/F)	30
Visser et al. (2001)	Flightiness Sensitiveness Willingness to perform Patience	Experiment (C)	41
Visser et al. (2003)	Patience Willingness to perform	Experiment (C/D) Observer rating	18
Wolff et al. (1997)	Gregariousness Fearfulness	Experiment (C)	42
Wolframm and Meulenbroek (2012)	Emotional reactivity Intelligence Gregariousness Willingness to work	Observer rating	2525

In an effort to maximise repeatability and interspecific comparison, several studies designed their research to incorporate variations of the Five Factor Model developed for assessing human personality (Costa Jr. and McCrae 1992, Morris, Gale, and Duffy 2002, Morris, Gale, and Howe 2002, Lloyd et al. 2007, McGrogan et al. 2008, Wolframm and Meulenbroek 2012, Ijichi et al. 2013). Of the five factors, 'neuroticism' and 'extraversion' and 'agreeableness' were most frequently found in horses (Morris, Gale, and Duffy 2002, McGrogan et al. 2008) while 'openness to experience' and 'conscientiousness' were difficult to both define and detect (Morris, Gale, and Duffy 2002). Variations of bold/shy and calm/nervous descriptors were the most common in the studies reviewed (Table 2.1), followed by gregariousness. Bold/shyness and calm/nervousness was usually assessed using novel object and handling tests (see citations in Table 2.1). Gregariousness was assessed either by rater opinion (Wolframm and Meulenbroek 2012, Ijichi et al. 2013) or by the horse's response to a social isolation test (Le Scolan et al. 1997, Wolff et al. 1997, Lansade, Bouissou, et al. 2008b, Lansade and Simon 2010, Valenchon et al. 2013, Lansade et al. 2016). Anderson (1999) and Seaman (2002) did not reduce results to personality traits, but instead looked for significant relationships between individual horse characteristics and reactivity to tests. Experimental assessments and ethological coding were sometimes used to test the reliability of observer ratings (Le Scolan et al. 1997, Lloyd et al. 2007, Ijichi et al. 2013)

The primary focus of all the studies cited above was to assess the personality of horses relative to their interactions with humans, or their reaction to various activities necessary in a managed setting (ex: performance behaviour, behaviour before feeding, behaviour during maintenance tasks etc.). 'Open field' tests were sometimes used as a control for experiments (Seaman et al. 2002, Lloyd et al. 2007, Hausberger et al. 2011, Bulens et al. 2015) but were not used by any study as the sole method of assessing individual personality. Although Seaman et al. (2002) also included behaviour during reintroduction to a social group as part of their assessment, Briard et al. (2015) was the only study to examine domestic horse personality in the context of long-term unmanaged interspecific interactions. Briard et al. (2015) used observer rating to explore the relationship between personality and affiliative relationships in the collective movement of a herd of 37 one to six-year-old mares and fillies.

Baker (2015) was the only other study found to use non-manipulative methods to assess the personality types of equids living in natural social groups. In the broader field of animal personality study 'open field' and 'hands off' assessment methods remain uncommon, particularly in mammals (Bremner-Harrison et al. 2017). Baker (2015) used ethological coding and experimental assessment to identify nine personality traits; 'assertiveness', 'sociality', 'activeness', 'extroversion', 'neuroticism', 'aggression', 'exploration', 'boldness', and 'inquisitiveness'. The traits were found to be significantly associated with multiple demographic and life history characteristics, including age, sex, health, reproduction, group size, and position within group.

2.1.4. Personality and conservation

Conservation work very often involves working with threatened or endangered species with small and isolated populations, where the variation in individual fitness and survival can have a profound impact on the population as a whole (McDougall et al. 2006). Multiple papers have recommended incorporating personality assessment into reintroduction or translocation protocols to maximise the survival and adaption of individuals once released (Bremner-Harrison et al. 2004, McDougall et al. 2006, Watters and Meehan 2007). Reintroduced swift foxes (*Vulpes velox*) assessed as bold had lower survival after reintroduction than shy individuals (Bremner-Harrison et al. 2004). However, bold Tasmanian devils (*Sarcophilus harrisii*) had higher survival following reintroduction than shy individuals (Sinn et al. 2014). Stratton (2015) found higher survival overall in release groups of wood mice (*Apodemus sylvaticus*) composed of a mix of bold and shy individuals than in groups composed entirely of bold or entirely of shy individuals.

Personality phenotypes can be heritable (Dingemanse et al. 2003, Reale et al. 2007) and are thought to persist in populations because behavioural diversity gives species more flexibility in adapting to fluctuating environments (Reale et al. 2007, Bergmueller and Taborsky 2010). Personality traits have been found to influence the fitness of mammals, birds, fish, reptiles, and insects (Cote et al. 2008, Smith and Blumstein 2008).

The sociability scores in wild populations of yellow-bellied marmots were positively correlated to yearling production and recruitment (Armitage 1986). For female yearling marmots, individuals with higher sociability scores were less likely to disperse from their natal groups (Blumstein et al. 2009). Sociability scores also influenced the fitness of common lizards (*Lacerta vivipara*). Lizards with low sociability scores were found to survive better in low density populations and females with higher sociability scores had a higher probability of reproducing, regardless of population density (Cote et al. 2008).

Other personality traits that have been demonstrated to influence fitness in wild populations are boldness and docility in bighorn sheep (*Ovis canadensis*) (Dingemanse and Reale 2005), exploration in great tits (*Parus major*) (Dingemanse et al. 2004, Dingemanse and Reale 2005), and aggression in bluebirds (*Sialia sp.*) (Duckworth and Badyaev 2007). Bolder and more docile bighorn ewes were found to reproduce at an earlier age than shy and non-docile ewes (Dingemanse and Reale 2005). During periods of high predation pressure, young or bold ewes had higher survival rates than old or shy ewes (Dingemanse and Reale 2005).

Exploration scores (slow vs fast exploring) influenced the survival of great tits, depending on their sex, their parents' sex and exploratory type, and the availability of beech (*Fagus sylvaticus*) mast in a given year (Dingemanse et al. 2003, 2004, Both et al. 2005, Dingemanse and Reale 2005). In beech masting years, fast exploring males and slow exploring females, and juveniles of either extreme of personality had higher survival (Dingemanse and Reale 2005). In non-masting years, slow exploring males, fast exploring females, and juveniles with intermediate exploration speeds had the highest survival (Dingemanse and Reale 2005).

Duckworth and Badyaev (2007) found a high occurrence of highly aggressive western bluebird (*Sialia mexicana*) males at the frontier edge of their range expansion, where they competed with and displaced mountain bluebirds (*Sialia currucoides*). Once western bluebirds became established and competition with mountain bluebirds ceased, the occurrence of highly aggressive males decreased because highly aggressive males had lower parental investment and thus lower offspring recruitment than less aggressive males (Duckworth and Badyaev 2007).

All these studies demonstrate the effect that personality can have on individual fitness, intra- and interspecific interactions, and species diversity and adaptability.

2.1.5. Applicability of personality research to takhi conservation

Future management of takhi populations will involve maximising the survival of the species in a highly competitive environment where they must cope with resource overlap with humans and livestock and risk of hybridisation with domestic horses (Moehlman et al. 2016). As takhi populations grow, their home ranges will expand outside of protected reintroduction sites and they will come in more frequent contact with domestic horses. Population growth and expansion will also make the current practise of daily monitoring of all takhi family groups less logistically feasible. Future management of takhi populations will need to include development of an understanding of how and why takhi social groups form, and the role which each individual plays in shaping overall structure. Part of understanding the role of the individual includes improving knowledge of how individuals vary, not only in term of easily defined demographic data, but also relative to individual behavioural and social traits and tendencies. An understanding of the influence of the individual on overall social structure may make it possible to identify high risk groups or individuals (those most likely to disperse or come into contact with domestic horses), and design management decisions to promote cohesiveness within takhi groups and herds.

The aim of this chapter was to develop methodology for identifying consistent and repeatable personality traits in free living takhi and explore demographic trends in personality types. Takhi personality was assessed for all individuals in focal family groups at the Seer and Hustai reintroduction sites (Chapter 1, section 1.4; Chapter 3, section 3.2.1.1.) using observer rating by rangers and ethological coding of natural behaviour.

2.2. Methods

The Seer and Hustai study sites are described in detail in Chapter 1, section 1.4. The individuals of the focal family groups are described in Chapter 3, section 3.2.1.1.

2.2.1. Observer ratings

2.2.1.1. Survey design

The observer rating assessments went through several stages of development. The initial draft questionnaire was comprised of adjectives drawn from several studies (Creighton, unpublished data, Gosling and John 1999, Lloyd et al. 2007, Lee and Moss 2012). Upon some discussion with rangers at Seer, however, it became clear that some of the adjectives rangers were asked to respond to had limited cultural context in Mongolia. All the Seer rangers were therefore asked to write a list of adjectives they might use to describe the Seer takhi. The adjectives generated by rangers and some additional adjectives from the literature were incorporated into a second draft of the assessment (Appendix 2.I). Assessments (one assessment sheet per takhi per ranger) were given to Seer rangers to complete. Some rangers found this format to be too restrictive and the lack of definitions for adjectives confusing. The assessments were therefore revised again, this time modelled on the assessments used by Williams (2013). Rangers and biologists at both Seer and Hustai rated the personalities of takhi in the focal family groups using a questionnaire listing and defining 30 adjectives describing takhi character traits (Table 2.2). Raters used a visual analogue scale to rate how strongly they felt each takhi displayed each character trait, ranging from 0 (not at all) to 10 (the epitome of the trait) by marking along a 10-cm line segment.

Table 2.2. Final version of assessment used to investigate takhi personality using observer ratings.

Takhi Name: ____________________ Takhi ID: _______
Your Name: _________________________
How many months (years) have you observed this takhi? _______________
What years did you observe this takhi? _________________

Please assess how much you feel this horse exhibits each of the defined character traits below, by marking on the line how strongly the horse exhibits this character type.

0=Does not have this character type, 5 = Displays this character type to a middling degree, **10**=Strongly exhibits this character type

Example

Sensitive –Reacts strongly and easily to other takhi or surroundings.

0 ✕ 10

Active – Moves around frequently. Keeps 'busy.'

0 10

Adaptable – Adapts quickly to new situations

0 10

Aggressive – Frequently acts aggressively towards other takhi.

0 10

Calm – Is quiet and relaxed. No easily disturbed or upset.

0 10

Confident – Is positive, assured, and relaxed. Is not restrained or tentative.

0 10

Curious – Is interested in new objects or situations.

0 10

Defensive – Is very protective of self or offspring. Often wary of the approach of other takhi.

0 10

Dominant – Asserts authority over other takhi.

0 10

Gentle – Reacts kindly and patiently to other takhi. Rarely behaves aggressively

0 10

Good character – Is an upright herd member with good morals. Makes positive contributions to the herd.

0 10

Grazes at centre of family group

0 10

Grazes at edge of family group

0 10

Grazes at front of family group

0 10

Impulsive – Will react suddenly/unexpectedly to novel or familiar situations.

0 10

Insecure – Doesn’t like to act alone. Frequently relies on other takhi.

0 10

Irritable – Reacts negatively to other takhi with little provocation

0 10

Joyful – Has a cheerful character. Rarely angry.

0 10

Leader – Is frequently the first to change activity and is followed by other takhi.

0 10

Mischievous – Often disrupts other takhi with play behaviours.

0 10

Nervous – Worries. Is easily frightened.

0 10

Opportunistic- Acts quickly on opportunities when they appear.

0 10

Patient – Tolerant of other takhi, especially younger horses.

0 10

Playful – Frequently initiates and participates in play.

0 10

Popular – Interacts positively and frequently with other takhi.

0 10

Predictable – Has consistent behaviour patterns.

0 10

Protective - Takes care of other takhi. Is a ‘safe place’ for others takhi.

0 10

Sensitive –Reacts strongly and easily to other takhi or surroundings.

0 10

Smart – Exhibits optimal behaviour choices. Is alert to surroundings and responds quickly and correctly to challenges.

0 10

Social – Prefers to be in close company with others. Does not spend time away from other takhi.

0 10

Vigilant – Frequently monitors surroundings. Is usually alert.

0 10

Other comments about this takhi?

2.2.1.2. Monitoring practises at Seer and Hustai

Seer rangers conduct hour-long observations of two of the three family groups (four later in 2015) daily, alternating each day between morning and evening observations. In the fall, spring, and summer, an additional location and group composition check was conducted, including locating individuals not part of the larger herd. At Hustai, rangers performed daily checks of each family group, recording the location of each group, changes in group membership, and health problems (Ts. Lhavgadorj, pers. comm. 2015). Ranger rating assessments were given to six rangers and biologists at Seer, and to three at Hustai.

2.2.1.3. Checking rater agreement

Rater agreement in ranking of takhi for each adjective and the ranking of adjectives for each takhi was checked using Kendall's coefficient of concordance (W) in StatXact (Cytel Software 2015). Results were considered significant if $p \leq 0.05$. Tests for agreement by adjective and by takhi were run separately for each field site. The agreement of rater pairs was also checked, to determine if one rater consistently disagreed with other raters in their rating of takhi across adjectives. Spearman's rank order correlation coefficient was used to check for agreement between rater pairs for each adjective.

2.2.1.4. Factor analysis

Adjectives and takhi with significant agreement between raters were incorporated into a factor analysis. Factor analysis (FA) detects latent constructs in datasets that account for correlations between variables, in this case adjectives (Budaev 2010). These constructs, extracted as factors, can be interpreted as personality descriptors (Budaev 2010, Koski 2011, Stratton 2015). FA is preferable to principal components analysis (PCA: another data reduction method commonly used in personality research) because the FA model includes an error term, while PCA assumes that the dataset is the source for all variation in the model (Budaev 2010). FA using principal axis factoring and a Varimax rotation was applied to the correlation matrix of the rating dataset using SPSS 23 (IBM Corp 2015, Budaev 2010). Parallel analysis was used to determine the number of factors to extract (Patil et al. 2008). The data were tested for suitability for factor analysis using the Kaiser-Meyer-Olkin measure of sampling adequacy (KMO) and Bartlett's test of sphericity (Budaev 2010). Factor scores for individual takhi were calculated using the regression method (Koski 2011, Stratton 2015).

2.2.2. Ethological coding

2.2.2.1. Ethogram design

A coding ethogram was developed through combining ethograms created previously by the Seer research team (Association Takh, unpublished data), Bremner-Harrison et al. (2004), and

McDonnell (2003). The initial ethogram included 52 behaviours but was ultimately expanded to include 80 behaviours as additional behaviours were observed during sampling (Appendix 2.II).

2.2.2.2. Data collection

Ethological coding data were collected during one-hour observation periods, using scan sampling (Altmann 1974) to record the behaviour and nearest neighbour of all takhi present in the focal group. Scan sampling was used instead of focal animal or all occurrences sampling because the method allowed the frequent and simultaneous sampling of all individuals in the social group under the same environmental and social conditions. A series of pilot observations were run, from which it was determined that a minimum interval of two minutes between scan samples was necessary to allow enough time to locate, identify, and record all individuals in the largest family group (19 individuals).

At Seer, the focal group was switched after one hour, and the observer repeated the same sampling procedure for a second hour of observation with another group. Seer personality observations were conducted at the beginning and end of the fall and spring field work periods, which ran from October through November, 2014 and March through April, 2015, respectively. At Hustai, data were collected over a shorter period (one week in May and one week in July, 2015). Hustai's terrain and larger takhi population made relocating individual groups more challenging, so on each day one focal group was followed for seven hours. During the seven hours, observations alternated between recording one hour of ethological coding scans and one hour of simultaneous observations (recording interindividual interactions and spatial distribution, described in Chapter 3, section 3.2.1).

2.2.2.3. Initial application of FA

Initially, FA was also applied to the analysis of the ethological coding. KMO tests indicated that the coding data were not suitable for factor analysis (KMO = 0.281), even when all major maintenance behaviours were removed from the data set (KMO = 0.456), and when only high frequency behaviours were considered (KMO=0.354). Because FA could not be applied to the dataset, behaviours were instead classed into categories reflecting their indication of individual sociability.

2.2.2.4. Categorizing behaviours

Behaviours observed during scan sampling were classed into three categories; non-social, positive social, and negative social. Non-social interactions included maintenance behaviours and any social interactions that were not clearly affiliative or offensive agonistic. Non-social behaviours were discarded from further analysis. Behaviours considered socially positive were actively affiliative interactions, such as play and allogrooming. Behaviours considered socially negative were offensive agonistic interactions, where individuals directed interactions towards conspecifics with the intention of displacing them. Eight behaviours were assigned to the positive social category and six were assigned to the negative social category (Table 2.3).

Table 2.3. Behaviours included in each behaviour category for the individual takhi sociability assessments. For behaviour definitions, see the ethological coding ethogram in Appendix 2.II.

Positive social	Negative social
groom conspecific	bite
mutual fly control	bite threat
play bite	charging conspecific
play chase	chasing conspecific
play flee	driving conspecific
play kick	head threat
play mount	
play other	

2.2.2.5. Calculating coded sociability scores and assessing reliability

For each hour-long observation period, the number of positive social and negative social behaviour occurrences were weighted prior to calculating the final sociability score. Positive social behaviour scores were given a weight of 1 and negative social behaviour scores were given a weight of -1. The weighted scores were summed and then divided by the total number of scan samples taken for each individual to give an overall sociability score for each takhi for each observation period. Individual sociability scores were checked for repeatability between each observation period using Kendall's coefficient of concordance in RStudio version 1.0.143 (RStudio Team 2016).

2.2.3. Comparing rating and coding scores and checking for demographic trends

Agreement between rated and coded sociability scores and the relationship between personality score and age were tested using Spearman's correlation coefficient. A significant difference in personality score based on sex was tested using a Wilcoxon-Mann-Whitney U test for two independent samples. Seer takhi had a skewed sex/age ratio among both adults and juveniles, with more adult females (mares) and more juvenile males (colts) (Table 2.4). Reproductive state, particularly in mares, can influence social and grouping behaviour (Rubenstein 1994, Boyd et al. 2016). Therefore, a significant difference in personality score based on reproductive class was also tested using a Kruskal-Wallis test for K independent samples and a Conover-Iman post-hoc multiple comparisons test with a Benjamini-Yekutieli p-value adjustment to determine where significant differences in personality score between reproductive classes occurred. All analyses were performed in RStudio version 1.0.143

(RStudio Team 2016). The Kruskal-Wallis and Conover-Iman tests used the package 'conover.test' (Dinno 2017).

Both male and female takhi reach behavioural maturity at around four to five years of age, with much variation among individuals (Monfort et al. 1994, Boyd et al. 2016). Males are behaviourally mature when they are capable of managing a family group, while females tend to show behavioural maturity after the birth of their first foal. In this study, all males older than 5 years present in the focal groups were family stallions, so the classification of colts and stallions was based strictly upon age. Female classification was more complex, as some fillies had dispersed and reproduced by four years of age, while some had not. Thus, additional criteria were used to define the reproductive class of female takhi. Any individuals nursing a foal at some point during the study period were classified as a 'lactating mare', regardless of age. All remaining females, those that did not nurse a foal at any point during the study period, were classified as non-lactating mares if they were older than five years, and as fillies if they were four years old or younger. Thus, for this study takhi were divided into five reproductive classes; mature stallion (male ≥ 5 years), lactating mare (female nursing a foal during the study period), non-lactating mare (female ≥ 5 years but not nursing a foal during the study period), colt (male ≤4 years), and filly (female ≤4 years and not nursing a foal during the study period). The number of individuals in each category is shown in Table 2.4.

Table 2.4. Number of Seer takhi for whom personality was assessed in each reproductive class.

Reproductive class	Count
Mature stallion	3
Lactating mare	11
Non-lactating mare	5
Colt	16
Filly	6
Total	41

2.3. Results

2.3.1. Observer ratings

2.3.1.1. Data collection

Six rangers and biologists at Seer (Raters 1, 2, 3, 4, 5, and 6) and three at Hustai (Raters 7, 8, and 9) completed takhi personality assessments. At Seer, raters 1, 3, 4, 5, and 6 all participated in the daily observations. Rater 2 had known the takhi the longest overall but had not regularly participated in daily observations within the last 10 years. Of the raters participating in daily observations, rater 6 had known the takhi the longest (40 months) and rater 3 had known the takhi for the shortest period (3 months) (Table 2.5). At Hustai, raters 7 and 8 participated in the daily group checks, while rater 9 was involved more in overall demographic research and no longer observed the takhi daily.

Table 2.5. Rater familiarity with takhi in focal family groups at Seer (raters 1 - 6) and Hustai (raters 7 – 9).

Location	Rater ID	Months known	Average time observing per day (hrs) in 2014/2015
Seer	1	9	2.25
	2	264	0
	3	3	2.25
	4	16	2.25
	5	28	2.25
	6	40	2.25
Hustai	7	96*	0.25
	8	Not reported	0.25
	9	91.2*	0

*Average values, as time known was given per takhi. The minimum time known for both rangers was 24 months, and maximum was 132 months.

Raters at Seer completed assessments for all takhi present in 2014 and 2015 ($n = 55$). Due to the larger population size and less intensive monitoring practises, raters at Hustai did not know all focal Hustai group members well as individuals, so ratings from all three Hustai raters were only completed for the focal family stallions ($n = 5$).

2.3.1.2. Checking for agreement

2.3.1.2.1. Agreement between ranger pairs

Significant correlations at Seer for each pair of raters for each adjective generally had a correlation coefficient ≥0.3. The number of significant agreements each rater had with any other rater were summed to estimate each rater's overall agreement with other raters (Table 2.6). Rater 1 had the highest frequency of agreement, being part of 64 high agreement pairs. Rater 3 had the lowest overall frequency of agreement, being part of 47 high agreement pairs. Rater 2 had the second lowest frequency of agreement, being part of 48 high agreement pairs. Given that rater 2 had the second lowest agreement frequency, had also scored only 14 of the 55 Seer takhi, and had only observed the takhi at one time during the study period, rater 2's ratings were removed from further analyses.

Hustai raters 7 and 8 had significantly correlated scores for the adjectives 'Opportunistic', 'Popular', 'Smart', and 'Social.' Raters 8 and 9 were significantly correlated for 'Grazes at centre' and 'Popular'. Raters 7 and 9 had no significant correlation for any of the adjectives.

Table 2.6. Frequency of incorporation in high agreement pairs for each Seer rater. The number in parentheses shows the percentage of total possible pairs, which was 30 adjectives X five other raters, or 150. High agreement pairs were those with a Spearman's correlation coefficient of >0.3 for the ranked scoring of takhi by adjective.

Rater	Pairs
1	64 (42.7)
2	48 (32.0)
3	47 (31.3)
4	57 (38.0)
5	63 (42.0)
6	53 (35.3)
Total possible pairs	150

2.3.1.2.2. Agreement by adjective

Hustai rater agreement was only significant by takhi for two takhi, and only significant by adjective for one adjective. Hustai rating data was therefore considered insufficiently rigorous to be included in further analysis.

Considering only Seer takhi, of the 30 adjectives included in the assessment (Table 2.2), there was significant agreement ($p \leq 0.05$) in ranger ratings for each takhi for 26 adjectives. There was no significant agreement for the adjectives 'Curious', 'Insecure', 'Nervous', and 'Patient,' so these adjectives were removed from further analysis. Of the 55 Seer takhi, there was significant agreement in ranger adjective scores for 44 individuals. Raters did not agree on ratings for three adult mares (CH, GH, and SS) or for eight of the ten 2015 foals. The three mares and all 2015 foals were removed from further analysis, leaving 41 takhi descriptions to incorporate into the FA.

2.3.1.2.3. Checking rater agreement across opposites

Eight adjectives in the questionnaire formed five pairs of descriptor opposites; 'Aggressive' and 'Gentle', 'Calm' and 'Nervous', 'Confident' and 'Nervous', 'Confident' and 'Insecure', and 'Grazes at edge' and 'Grazes at centre'. Three of the pairs included adjectives removed from analysis due to low agreement between raters ('Insecure' and 'Nervous'). The two remaining pairs, 'Aggressive' vs 'Gentle' and the relative grazing positions, were checked for rater consistency across opposite terms. Rater scorings on opposite adjectives for each horse were summed, to determine if rangers were consistent in assigning a low score to one adjective and a high score to it's opposite (Figure 2.1).

a)

N	203
Mean	0.998
St Deviation	0.208
Min	0.392
Max	1.566

b)

N	203
Mean	1.042
St Deviation	0.203
Min	0.212
Max	1.519

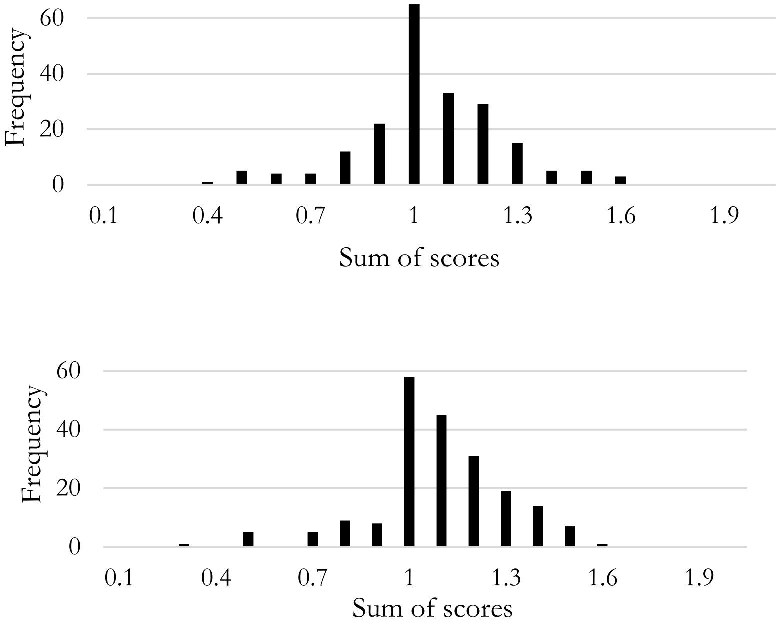


Figure 2.1. The frequency distribution of summed rater scorings for individual takhi for the opposite adjectives a) 'Aggressive' and 'Gentle' and b) 'Grazes at the edge of group' and 'Grazes at the centre of group'.

The frequency distribution of summed scores for both pairs of opposite adjectives centred around a mean of one with a standard distribution of about two points along the 10-point scale used by raters. Raters appeared to be consistent in their assessment of takhi across opposing personality descriptors. If a takhi was rated highly aggressive or likely to be found at the edge of a group, it was also rated as not very gentle, or unlikely to be found at the centre of the group.

2.3.1.3. Factor Analysis

Data suitable for FA have a KMO value ≥0.5 (for small sample sizes, ≥0.7) and a Bartlett's test score significant at $p \leq 0.05$ (Budaev 2010). For this data set KMO = 0.757 and Bartlett's = 1128.45, df = 325, $p < 0.000$, so the dataset was considered suitable for FA.

Two factors were extracted based on the results of parallel analysis (Patil, et al. 2007) and visual examination of the scree plot (Figure 2.2). The two factors extracted explained 63.2% of variation in the data; 43.4% (33.8% with rotation) and 19.8% (29.4% with rotation) for factors 1 and 2, respectively.

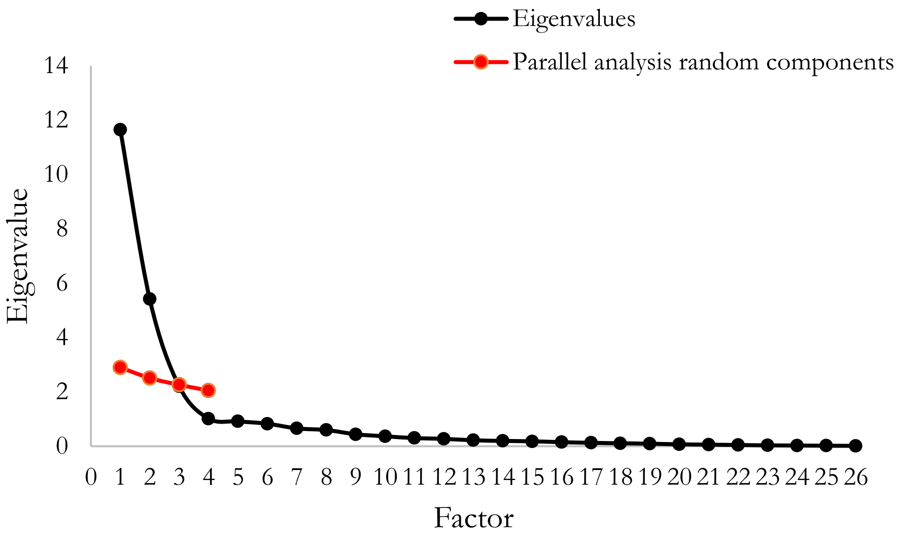


Figure 2.2. Scree plot displaying factor extraction cut-off justification for factor analysis of Seer ranger takhi personality ratings using parallel analysis, comparing observed eigenvalues to those calculated from random data. The black eigenvalue points represent the eigenvalues calculated from the observed data, and the red points represent eigenvalues generated from a random dataset with the same number of observations as the observed dataset using a parallel analysis engine (Patil et al. 2007).

The rotated factor matrix (Table 2.7) was examined for adjectives with loadings >0.6 and <-0.6 for Factors 1 and 2 (Budaev 2010). The Varimax rotation resulted in high loadings for 12 adjectives on Factor 1 and nine adjectives on Factor 2.

Table 2.7. Factor matrix of adjective loadings for a principle axis factor analysis with Varimax rotation. Variables highlighted in green have a loading score >0.6. Variables highlighted in red have a loading score <-0.6.

Adjective	Sociability (Factor 1)	Assertiveness (Factor 2)
Active	-.611	.281
Adaptable	.480	.503
Aggressive	-.686	.557
Calm	**.863**	.060
Confident	.250	**.871**
Defensive	-.533	**.708**
Dominant	-.307	**.864**
Gentle	**.902**	.013
Good character	**.927**	-.044
Grazes at centre	.685	-.217
Grazes at edge	-.612	.465
Grazes at front	-.551	.224
Impulsive	-.695	.424
Irritable	**-.753**	.404
Joyful	**.795**	.118
Leader	-.401	**.824**
Mischievous	.231	-.407
Opportunistic	-.280	**.764**
Playful	.450	-.450
Popular	.529	.218
Predictable	-.061	**.721**
Protective	.080	**.903**
Sensitive	-.625	.502
Smart	.318	.594
Social	**.782**	-.196
Vigilant	-.393	**.798**

Factor 1 had high positive loadings for adjectives that described a friendly or social personality and high negative loadings for adjectives that described a grumpy or antisocial personality (Table 2.8). Factor 2 had high positive loadings for adjectives that described an assertive or supervisory personality (Table 2.8).

Table 2.8. High scoring adjectives for rated Seer takhi personality from factor analysis. Adjectives in bold had a loading score >|0.7|.

Sociability (Factor 1)	Assertiveness (Factor 2)
Not active	**Confident**
Not aggressive	**Defensive**
Calm	**Dominant**
Gentle	**Leader**
Good character	**Opportunistic**
Grazes at centre	**Predictable**
Doesn't graze at edge	**Protective**
Not impulsive	Smart
Not irritable	**Vigilant**
Joyful	
Not sensitive	
Social	

As a rough litmus test, the regressed factor scores were visually assessed and compared with knowledge of the individual takhi. For the ‘sociability’ factor (Factor 1), the takhi with the highest scores were consistently takhi observed to be ‘friendly’ and ‘social’ with other takhi, while takhi with lower scores were generally those more frequently observed to interact negatively with other takhi. The exception was the family stallion CR, who had a low sociability score (Figure 2.3a), although he was frequently observed to play with the young colts from all three family groups. His low score is probably because many of the rangers considered him to be more aggressive than the other two stallions when managing his family. The takhi with negative scores for assertiveness (Factor 2) were all young or juvenile takhi with low status within their families (Figure 2.3b). The takhi with the highest assertiveness scores were those with higher status and more experience in the family groups (Figure 2.3b). Of the juveniles, YO and TA had the highest assertiveness scores (Figure 2.3b). TA in the spring and YO in the summer of 2015 became the most dominant of the juveniles in their post-dispersal social groups in 2015.

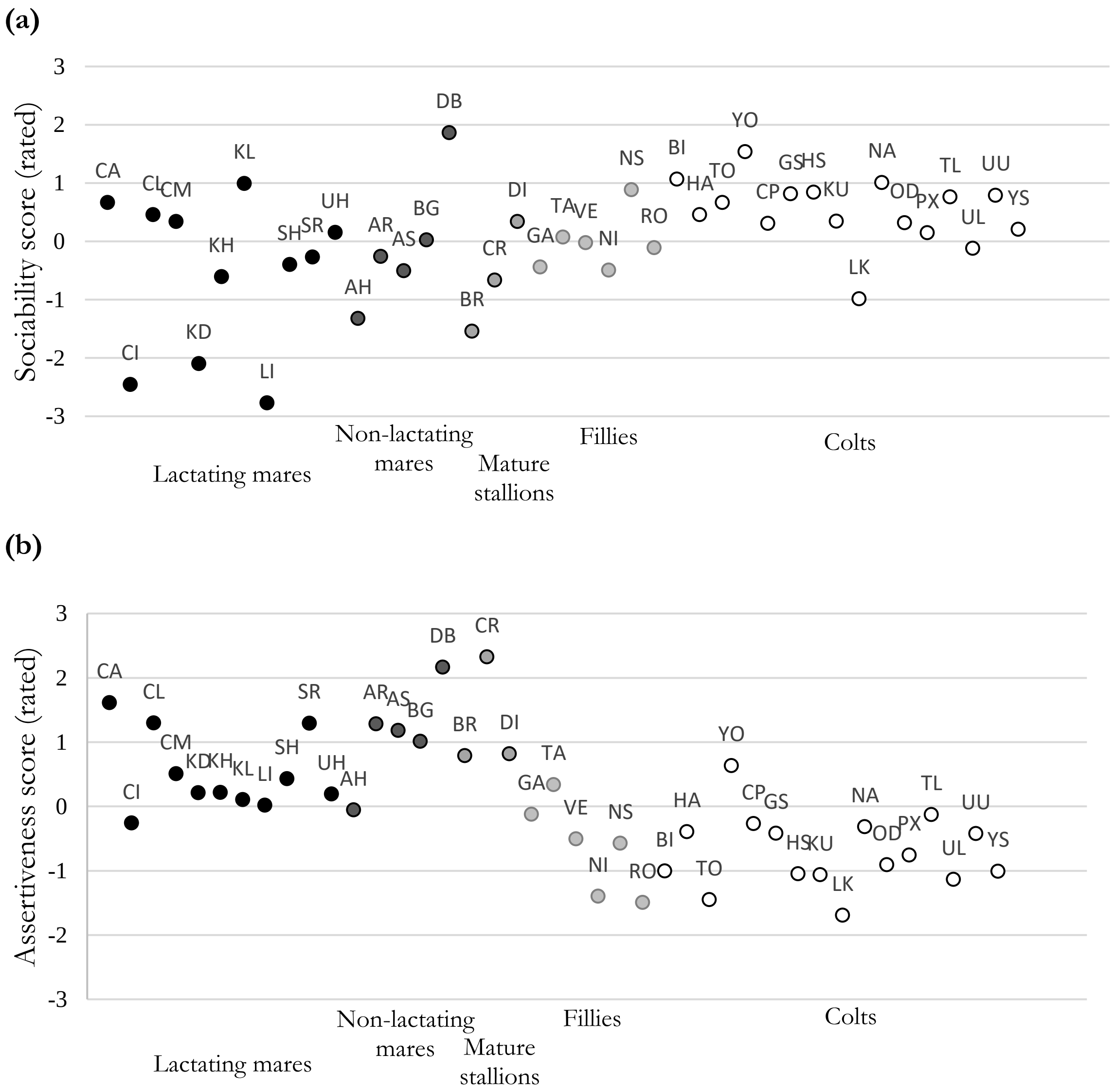


Figure 2.3. Plot of takhi (a) sociability and (b) assertiveness scores based on observer ratings. Solid black points are lactating mares, dark grey points are non-lactating mares, medium grey points are stallions, light grey points are fillies, and white points are colts.

2.3.2. Ethological coding

2.3.2.1. Data collected

The total hours of scan sampling (with 31 scan samples per hour) collected for each focal family group at Seer and Hustai are shown in Table 2.9. The OTHER group was formed by an independent mare and dispersing juveniles in the spring of 2015, so observation of that group was not conducted until April, 2015. Eight different positive social and six negative social behaviours were observed during scan sampling.

Table 2.9. Hours of scan sample observation for ethological coding per group per month at Seer and Hustai in 2014 and 2015. *Group IDs and group membership are defined in Chapter 3, section 3.2.1.1 and Appendix 3.II.

Location	Group ID*	October	November	March	April	May	July
Seer	BRG	2	2	2	2	-	-
	CRG	3	2	2	2	-	-
	DIG	2	2	3	2	-	-
	OTHER	-	-	-	4	-	-
Hustai	BDG	-	-	-	-	3	3
	DNG	-	-	-	-	3	3
	KEG	-	-	-	-	3	3
	WNG	-	-	-	-	3	3
	ZRG	-	-	-	-	3	3

2.3.2.2. Repeatability

Seer takhi showed significant repeatability in sociability scores across the four time intervals (W = 0.338, p=0.037). Hustai takhi did not show significant repeatability in scores across all personality scans (BDG: W=0.178, p=0.3942; DNG: W=0.189, p=0.3403; KEG: W=0.182, p=0.2527; WNG: W=0.124, p=0.5845; ZRG: W=0.254, p=0.1947) or within the observation intervals (Table 2.10), and so were excluded from further analyses.

Table 2.10. Repeatability of coded sociability scores calculated for takhi in Hustai family groups in the May and July, 2015 observation blocks. *Group IDs and group membership are defined in Chapter 3, section 3.2.1.1 and Appendix 3.II.

	May		July	
Group*	W	p-value	W	p-value
BDG	0.460	0.1691	0.120	0.9690
DNG	0.552	0.0555	0.333	0.4731
KEG	0.179	0.7181	0.375	0.3621
WNG	0.333	0.4571	0.371	0.3915
ZRG	0.333	0.4571	0.250	0.6134

2.3.2.3. Final scores

Given the significant repeatability of the sociability scores for the Seer takhi, the scores for each takhi for each time interval were summed, divided by the total number of scans for each individual, and then standardized to Z-scores to provide an overall coded sociability score for each takhi (Figure 2.4). Overall, CP and NA had the highest coded sociability score, and SR and BR had the lowest (Figure 2.4).

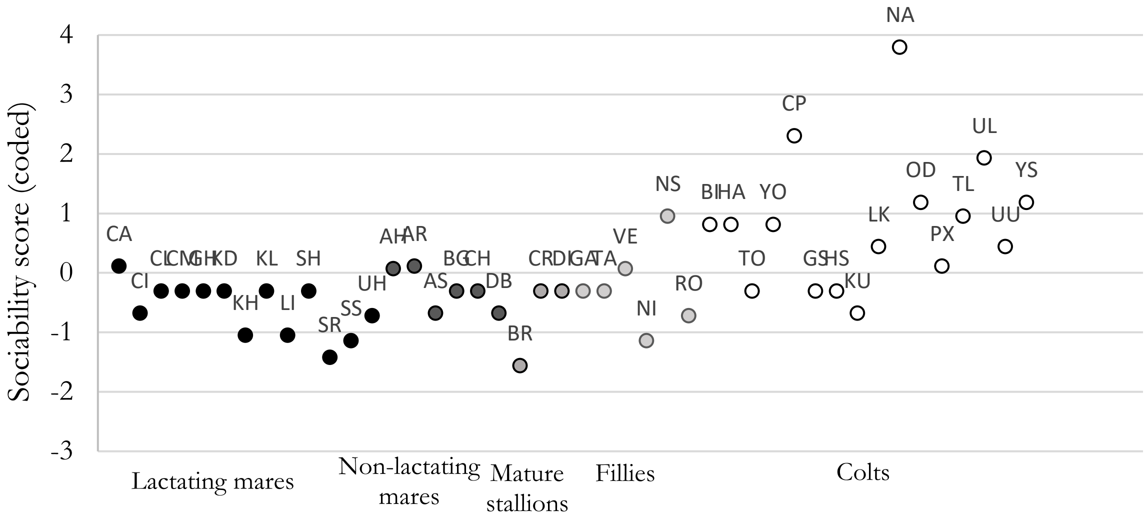


Figure 2.4. Plot of takhi coded sociability scores. Solid black points are lactating mares, dark grey points are non-lactating mares, medium grey points are stallions, light grey points are fillies, and white points are colts.

2.3.3. Comparability of rating and coding scores

The summed coding scores were compared with factor scores calculated for each takhi from the ranger ratings. There was a significant positive correlation between coded sociability scores and rated sociability scores for all assessed Seer takhi (ϱ=0.435, p=0.0045). There was a negative, but not significant, correlation between coded sociability scores and rated assertiveness scores (ϱ=-0.294, p=0.0616).

2.3.4. Demography of personality scores

Each Seer takhi was assigned three personality scores; a rated assertiveness score (Figure 2.3b), a rated sociability score (Figure 2.3a), and a coded sociability score (Figure 2.4). There was a highly significant positive correlation between takhi age and their assertiveness score (ϱ = 0.811, p<0.000) and a significant negative correlation between takhi age and both sociability scores (rated sociability, ϱ = -0.312, p=0.047; coded sociability, ϱ = -0.445, p = 0.002).

Males as a group had significantly higher sociability scores than females (rated sociability, U=124, p=0.026; coded sociability, U = 99, p=0.001). Females had a significantly higher assertiveness score than males (U = 311, p = 0.007).

The significant difference in male vs. female scores was partly due to the unbalanced sex ratio, particularly in takhi older than five years (Table 2.4). In 2015, 16% of males (n = 3) were older than five years while 76% of females (n =19) were over five years old. It therefore follows that females overall would tend to have significantly greater assertiveness scores, as assertiveness was strongly correlated with age. The takhi age/sex categories were therefore broken down further into reproductive classes, dividing the takhi in groups based on age, sex, and reproductive state.

There was a significant difference in personality score relative to reproductive class for all three personality scores (Table 2.11).

Table 2.11. Results of Kruskal-Wallis tests for a significant difference in personality score between reproductive classes for Seer takhi.

Personality score	H	df	p value
Rated assertiveness	25.95	4	**0.0000**
Rated sociability	9.31	4	**0.0500**
Coded sociability	18.33	4	**0.0000**

Overall, colts tended to have significantly higher sociability scores than lactating mares and adults tended to have higher assertiveness scores than juveniles (Table 2.12). For the coded sociability score, colts had significantly higher sociability scores than lactating mares. For the rated sociability score, once a Benjamini-Yekutieli adjustment for multiple comparisons was applied, no significant difference in pairwise scores was detected, although prior to adjustment, colts had significantly greater rated sociability scores than all other reproductive classes. For the rated assertiveness score, adults (stallions, lactating mares, and non-lactating mares) had significantly higher scores than juveniles (colts and fillies) (Table 2.12).

Table 2.12. Comparisons of personality score relative to reproductive class in Seer takhi using Conover-Iman's post-hoc multiple comparisons test with a Benjamini-Yekutieli adjustment of p-values. A positive test statistic (T) indicates that the group labelled in the column had a higher distribution than the group labelled in the row. A negative test statistic indicates that the group labelled in the row had a higher distribution than the group labelled in the column. 1 = mature stallion, 2 = lactating mare, 3 = non-lactating mare, 4 = colt, and 5 = filly. Significant p-values in bold.

Rated Sociability

Reproductive state		1	2	3	4
2	*T*	-0.57			
	p-value	1			
3	*T*	-0.63	-0.16		
	p-value	1	1		
4	*T*	-2.24	-2.65	-1.86	
	p-value	0.2284	0.1738	0.3473	
5	*T*	-0.75	-0.30	-0.11	1.85
	p-value	1	1	1	0.2681

Coded sociability

Reproductive state	1	2	3	4
2	-0.09			
	1			
3	-0.91	-1.18		
	0.7739	0.7208		
4	-3.04	-4.96	-2.66	
	0.0307	**0.0002**	0.0415	
5	-0.85	-1.09	0.07	2.75
	0.735	0.6859	1	0.0444

Rated Assertiveness

Reproductive state		1	2	3	4
2	*T*	1.34			
	p-value	0.3969			
3	*T*	0.35	-1.14		
	p-value	1	0.4829		
4	*T*	4.97	5.76	5.60	
	p-value	**0.0001**	**0.0000**	**0.0000**	
5	*T*	4.16	4.08	4.43	-0.39
	p-value	**0.0006**	**0.0006**	**0.0003**	1

2.4. Discussion

The methods applied in this study represent a non-invasive strategy for assessing personality traits in takhi; a large, endangered, group-living ungulate. Ethological coding and observer rating methods were used to identify significant and repeatable sociability and assertiveness personality traits in takhi. Results were consistent with those of Baker (2015), who also found that assertiveness and sociability traits explained the greatest amount variation in the behaviour in her study population.

Repeatable and correlated sociability traits were identified using both ethological coding and observer ratings. Sociability is defined in the personality literature as the tendency to seek contact with conspecifics, and/or the reaction to the presence or absence of conspecifics (Lansade, Bouissou, et al. 2008b, Koski 2011, Neumann et al. 2013, Briard et al. 2015) and is one of the five main categories of personality traits listed by Reale et al. (2007). The sociability trait found in this study is a melding of the personality traits 'aggressiveness' and 'sociability' defined by Reale et al. (2007), who separated agonistic and affiliative interactions into two separate traits, rather than maintaining a continuous score ranging from very antisocial to very social behaviours. Ethological coding sociability scores were based on the type of interactions individual takhi engaged in, ranging from antisocial (engaging only in agonistic and aggressive interactions) to social (engaging only in affiliative interactions) while the observer rated sociability scores were based on descriptive adjectives. The correlation between the scores using both methods of assessment suggests that sociability, as the tendency of individuals to seek or not seek interactions with and proximity to conspecifics, is a consistent personality trait in takhi.

Previous assessments of sociability in domestic horses were primarily in the context of isolation tests and horse/handler relationships, rather than horse/horse relationships. Isolation tests are an efficient but very specific way to assess sociability (Le Scolan et al. 1997, Lansade, Bouissou, et al. 2008b, Valenchon et al. 2013), as they determine the social dependence of an individual in a potentially stress-inducing situation. The reaction of domestic horses to the presence or absence of conspecifics and their relationship to humans is often of primary importance to human handlers, as strong reactions to isolation and to humans affect horse performance and the safety of horse and handler. Only one of the studies listed in Table 2.1, Ijichi et al. (2013), assessed sociability in the context in horse/horse relationships. Thus, the personality trait sociability (or gregariousness, or extroversion or agreeableness) as described in studies of domestic horses often came from a different context than the sociability observed in takhi in this study. However, the independent detection of sociability at Seer and at Le Villaret (Baker 2015) supports the conclusion that in a horse/horse context, as well as a horse/human context, sociability is a distinct and repeatable equine personality trait.

Observer rating methods for this study identified a second significant personality trait, assertiveness. Assertiveness has been identified as a personality trait in spotted hyena (*Crocuta crocuta*), brown capuchin monkeys (*Sapajus spp.*), chimpanzees (*Pan troglodytes*), orangutans (*Pongo spp.*), and rhesus macaques (*Macaca mulatta*) (Gosling 1998, Morton et al. 2013, Lefevre et al. 2014). Lee and Moss (2012) found a 'leadership' component in their analysis of African elephant (*Loxodonta africana*) personality with essentially the same definition as was applied for assertiveness in this study. Assertiveness is a challenging personality trait to define because it is closely related to dominance rank, and is very similar to the 'dominance' personality trait described in some primates (King and Figueredo 1997, Weiss et al. 2011, Morton et al. 2013). Gosling and John (1999) suggested that dominance or assertiveness, as well as activity, should be considered as viable dimensions of animal personality, even though they are not part of the human personality model. The non-primate literature has generally considered dominance to be a relative measure of the relationship between individuals (Drews 1993), and thus an emergent property of other personality traits, rather than a personality trait itself (Reale et al. 2007).

Adult takhi at Seer had significantly higher assertiveness scores than the juveniles, both when considering age as a continuous variable and when takhi were categorised by reproductive class (Table 2.12). In takhi, the oldest individuals are usually more dominant (King et al. 2016). It is not possible to know whether the assertiveness scores calculated in this study truly reflect individual personality traits, or are merely describing the herd dominance hierarchy as perceived by the observers. To confirm assertiveness as a personality trait in takhi, it would be necessary to check for consistency in assertiveness over time and across changes in reproductive state.

2.4.1. Takhi personality relative to age and sex

Both the sociability and assertiveness scores of takhi were related to the individual's sex, age, and reproductive state. The most strongly significant trend in sociability was that lactating mares tended to be the least social and colts tended to be the most social. Stallions, non-lactating mares, and fillies had scores more arrayed between the two (Figure 2.3a, Figure 2.4). Adults were significantly more assertive than juveniles. Baker (2015) also found a positive correlation between age and assertiveness, and a negative correlation between age and sociability, although she found no differences in personality score relative to sex.

Differences in personality depending on age and sex have been found in other personality studies. Chimpanzees of both sexes became less extroverted (a factor including a gregariousness sub-component) and open and more agreeable and conscientious as they aged (King et al. 2008). Males were more aggressive, emotional, and impulsive than females, and females showed a significantly greater decrease in activity with increasing age (King et al. 2008). Bremner-Harrison et al. (2004) found no significant difference in swift fox boldness score in relation to sex, but found that adult foxes had significantly higher boldness scores than juveniles. Male snow leopards (*Uncia uncia*) were more exploratory during novel object tests (Gartner and Powell 2012). Female cheetahs (*Acyinonyx jubatus*) were rated as more tense and fearful than males (Wielebnowski 1999, Chadwick 2014). Wielebnowski (1999) also found that fearful cheetahs of both sexes were less likely to breed successfully, although Chadwick (2014) did not find a similar trend. Briard et al. (2015) found a significant correlation between age and dominance rank in their herd of domestic mares. Prior to using partial correlations, they found significant intercorrelations between age, boldness, and dominance rank.

The majority of the other domestic horse personality studies that investigated relationships between age, sex and personality trait found no significant relationship between personality trait score and either age or sex (Le Scolan et al. 1997, Hausberger et al. 2004, Lansade, Bouissou, et al. 2008a, McGrogan et al. 2008, Hausberger et al. 2011). Other studies did not report any tests for differences in personality relative to age or sex (Visser et al. 2001, 2003, Lloyd et al. 2007, Valenchon et al. 2013). Seaman et al. (2002) found no difference in personality scores based on sex, but did find that younger horses (5-12 years) approached both people and objects more quickly than did older horses (13-21 years). Wolff et al. (1997) reported no important differences in personality based on age or sex, but did detect some behaviour variation depending on both age and sex. They also found that offspring of the same stallion showed similar behaviours (Wolff et al. 1997). The lack of a relationship between age and sex and personality in the majority of the domestic horse studies may be because the horses sampled were usually either juveniles (0 – 3 years) (Wolff et al. 1997, Visser et al. 2001, Lansade, Bouissou, et al. 2008a) or adults/young adults (Le Scolan et al. 1997, Visser et al. 2003, Hausberger et al. 2004, Lloyd et al. 2007, McGrogan et al. 2008, Hausberger et al. 2011, Valenchon et al. 2013). Only three of the studies working with adult horses assessed stallions (Hausberger et al. 2004, McGrogan et al. 2008, Wolframm and Meulenbroek 2012). All others focused on mares and/or geldings. In the three studies including stallions, the ratio of stallions to mares and to geldings respectively was 1.14:1 and 0.70:1 for Hausberger et al. (2004), but 0.08:1 and 0.05:1 for McGrogan et al. (2008) and 0.07:1 and 0.07:1 for Wolframm and Meulenbroek (2012). Although not discussed in any of the papers, it is unlikely that many of the mares assessed had foals at heel. Thus, the lack of any relationship between age and sex relative to personality found in domestic horse personality research to date may be due to limited variation in the age and reproductive state of horses included in the studies.

In a survey of 1202 mares, 1228 geldings, and 82 stallions rated by their owners, Wolframm and Meulenbroek (2012) found that mares were significantly less gregarious than either geldings or stallions. These results are consistent with the findings of this study and with more general observations of equine behaviour. Adult mares only rarely engage in play behaviour (Sigurjónsdóttir et al. 2003), but both family and bachelor stallions do (Berger 1986, Boyd 1988b, King et al. 2016). Although there are exceptions (Cameron et al. 2008), most studies report that colts play more than fillies (Boyd 1988a, Sigurjónsdóttir et al. 2003, King et al. 2016). In equids there is a strong link between foraging and reproductive success in mares (Rubenstein 1994), and because quantity of food is more important for equids than quality (Schoenecker et al. 2016), time available for foraging is an important resource for mares (Rubenstein 1994). Access to both food and water is particularly important for pregnant and lactating mares, as they are essentially providing resources for two (both the mare and her foal) (Rubenstein 1994). For stallions, mares are the limiting resource for their reproductive success (Rubenstein 1994), and stallions generally spend significantly more time engaged in non-maintenance and social behaviours and less time grazing than do mares (Boyd 1988b, Rubenstein 1994). It therefore follows logically that females, particularly adult mares, will have lower sociability scores than males, particularly colts. For colts and stallions, social skills will be important for their reproductive success, while for fillies and mares, maintenance of social ties can be more of a passive activity with a focus instead on maximizing resource acquisition time.

2.4.2. Low repeatability in mares, foals, and Hustai takhi

No significantly repeatable personality scores were found for the Hustai takhi using either the ethological coding or observer rating methods. At Seer, there was also no significant repeatability for three mares and the majority of the 2015 foals when using observer rating methods. The lack of repeatability for the coding method at Hustai is probably due to a combination of the distribution of sampling periods and small sample size (six hours per group with three hours collected on one day and three hours recorded on one other day three months later) (Table 2.9). The lack of agreement between Hustai ranger ratings is probably because Hustai rangers no longer spend an extended period of time observing the family groups. The ranger's impressions of the stallions they assessed were therefore based on brief periods of observation, past experience, or, potentially, shared impressions. Raters 7 and 8 were responsible for patrolling separate parts of the park, and therefore knew best the takhi with home ranges within their patrol zone. Rater 9 no longer regularly observed takhi families in the field. For all these reasons, the lack of repeatability for the Hustai is not surprising.

The lack of repeatability in the 2015 Seer foal ratings was probably due to the timing and intensity of data collection. Seer scan samples were completed prior to summer foaling, so data were only available for the oldest 2015 foal. When the ranger ratings of the takhi were completed, the oldest 2015 foal (USR) was three months old and the youngest (UKH) had not yet been born. During the first month of life, takhi foals are highly dependent on their dam (Boyd 1988a). During the second month, they begin to feed more and nurse less, and start to interact more with other family members, including their peers (Boyd 1988a). The rapid development of social behaviour in takhi foals would make personality assessment of foals of staggered ages potentially biased, as they would all be in different and rapidly changing stages of social development. Repeatable and accurate assessment of foal personality would require intense, extended, and regular monitoring periods across all stages of early social development, using either coding assessment or rating methods.

Of the 44 takhi older than one year at Seer, one non-lactating mare (CH) and two lactating mares (GH and SS) had insufficient interobserver agreement to be incorporated in the FA. It is difficult to know why the Seer rangers had such differing opinions on these three mares. It may be that one ranger observed a mare in an extreme situation that left them with a strong impression of that mare's character, one which would not have been shared by the other rangers, as they were not present to witness the event. In Lloyd et al. (2007)'s study, 26 of 61 horses did not have significant agreement between raters, and of these 17 did not have significant agreement between even two raters. Lloyd et al. (2007) considered significant rater agreement on 44 of 61 horses (72.1%) to be a high rate of agreement. This study found significant agreement on 41 of 44 older takhi (93.0%) among five raters, suggesting the results presented here are, relatively, very robust. All three mares with non-repeatable rating scores had significantly repeatable coded sociability scores.

2.4.3. The limitations of applied methodology

Rater questionnaires were designed to capture the maximum amount takhi personality variation with a minimum of adjective descriptors, as raters were asked to assess over fifty individual horses and observer exhaustion was a concern. For this reason, deliberate descriptor opposites were not included in the questionnaire. For example, if 'Leader' was included as a descriptor, but 'Follower' was not. As a result, only two pairs of adjectives ('Aggressive' and 'Gentle' and 'Grazes at edge' and 'Grazes at centre') were available for checking rater consistency across opposite adjectives (section 2.3.1.2.3). An earlier version of the questionnaire asked rangers to mark on a line between to opposite adjectives, rather than from 0 to 10 (see Appendix 2.I). Although opposite adjectives were included, only a single measure resulted, rather than two opposite measures which would allow ratings to be compared. Thus, with neither version of the questionnaire was it possible to check for rater consistency across all descriptors. The inclusion of descriptor opposites in later versions of the questionnaire would add additional robustness to the results, as it would be possible to ensure that rangers were consistent in their perception and description of individual horses.

The rater questionnaire consistently presented the 0 to 10 scale with the 0 on the left and the 10 on the right. This arrangement could also produce rater bias if raters had a general tendency to mark more to the left or more to the right along the line. However, consistent ordering also made the questionnaire easier to use. Given the differences in first languages and language proficiency among raters, the benefits of questionnaire clarity may have outweighed the costs of potential lateral bias among raters in terms of dataset quality. For future use of rater questionnaires for assessing takhi personality, it may also be advisable to vary the starting side of the descriptor scale bars, sometimes locating the zero on the left and sometimes on the right, to reduce the risk of rater lateral bias. However, raters should be provided with clear written and spoken reminders of the format of the questionnaire, as failure to notice changes in the start point of the scale bar would render results useless and such mistakes would be impossible to detect.

The original aim of the ethological coding assessment of takhi personality was to use scan sampling to develop a representation of the behaviour of all takhi present in the focal group across the hours of observation. Data were collected with the intention of using factor analysis to extract personality traits based on the frequency of observed behaviours. By using factor analysis, the results would have been directly comparable to those obtained from the observer rating data. However, because the data were not suitable for factor analysis (Chapter 2, section 2.2.2.3) behaviours were classed for relative sociability instead. Instantaneous scan sampling was less suitable for this method of personality assessment, as assessment of sociability using classification was based on behaviour events, rather than behaviour states (Table 2.3, Altmann 1974). As a result, rates of occurrence for targeted behaviours were very low, reducing the reliability of the coded sociability assessments. It is recommended that further assessment of takhi personality based on rare event behaviours should use all occurrences sampling rather than scan sampling, to increase the size of the dataset from which sociability scores are assessed. Alternatively, scan sampling could still be applied to the simultaneous assessment of large groups, but many more hours of observation would provide a more robust dataset.

2.4.4. Potential applicability of personality research to takhi conservation

The results of this study suggest that both ethological coding and observer rating can be used to assess takhi personality, although >8 hours of observation per individual across multiple periods will be necessary to obtain repeatable and accurate ethological coding results. With larger sample sizes it may be possible to extract more personality traits in addition to sociability. As takhi populations continue to grow, it is unlikely that rangers will continue to know all takhi as individuals, as is already the case at Hustai, but observers conducting coding scans could also rate focal animals at the conclusion of data collection and prior to data analysis (Briard et al. 2015).

Documenting personality types in takhi may provide another key to the puzzle of how to manage what are essentially island populations of an endangered species surrounded by a sea of domestic horses, with their potential to flood and dilute the takhi genome if hybridisation begins to occur at too high a rate. Although testing is beyond the scope of this study, it is possible that personality profiles for individuals in reintroduced populations can be used to predict behaviour during dispersal, or during resource competition for mates or for food. The dispersal period for takhi is a particularly risky one from a conservation perspective. During their initial dispersal period, juveniles may travel over 50 km away from their family home range. With current distributions, the only equids they would encounter at that distance would be domestic horses. At Hustai, some dispersing takhi stallions that take up with domestic horse mares afterwards no longer show interest in takhi mares (D. Usukhjargal, pers. comm. 2015). These stallions then become essentially removed from the breeding population. Personality profiling may make it possible to assess which individuals possess low intraspecific cohesive tendencies and are at higher risk of long distance dispersal or domestic horse attachment. Careful monitoring of these individuals as they reach dispersal age may make it possible to redirect their dispersal movements towards other ‘available’ takhi. Personality profiling may also make it possible to predict family compatibility and stability, and allow managers and rangers to focus monitoring and management efforts.

2.5. Chapter Outcomes

The purpose of this chapter was to develop and apply non-interference methods of assessing takhi personality for later application in social network analysis. Significantly repeatable personality traits scores were extracted for Seer takhi, but not for Hustai takhi. At Seer, two personality traits were identified; sociability and assertiveness.

Main chapter findings were as follows:

- Significantly repeatable and correlated 'sociability' scores were extracted for Seer takhi older than one year using observer rating and ethological coding methods.
- Significantly repeatable 'assertiveness' scores were extracted for Seer takhi older than one year using observer rating methods.
- Personality trait scores could not be extracted for the Hustai takhi due to lack of repeatability in ethological coding data, and insufficient agreement in rating scores between rangers.
- There was a significant positive correlation between takhi age and assertiveness score, and a significantly negative correlation between takhi age and sociability score. Female takhi had significantly higher assertiveness scores and lower sociability scores than males.
- Colts tended to have significantly higher sociability scores than lactating mares, and adults of both sexes had significantly higher assertiveness scores than juveniles.

The following chapters will assess whether individual takhi personality score, along with other individual characteristics including group membership and reproductive state, has a significant influence on individual contribution to intra- and intergroup cohesion, as assessed through individual position in intra- and intergroup spatial and interaction networks.

3. Social network analysis - a brief review and applied methodology

3.1. Introduction to social network analysis

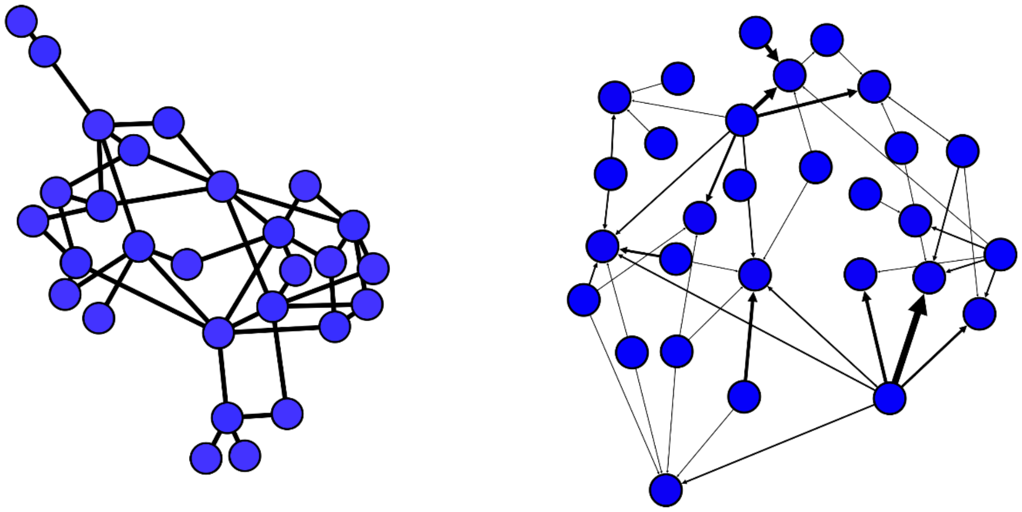
3.1.1. What are social networks?

Social network analysis (SNA) is a method of exploring animal social structure by looking at how connections between individuals shape the higher level social structure of a population or sample group (Whitehead 2008a, Krause et al. 2015). The two fundamental parts of a social network are '**nodes**' (sometimes called vertices) and '**links**' (sometimes called edges, ties, connections, or arcs) (Croft et al. 2008, Krause et al. 2015). (All terms in bold can be found in a glossary in Appendix 3.I). In a visual depiction of a network (a **sociogram**) (Figure 3.1) nodes are shown as points, and links are shown as the lines connecting those points. Nodes most commonly represent individuals in the study population. Each node can possess a series of **attributes** that describe the individual node. Attributes include common demographic descriptors such as sex, age, and group membership, but may also include node-level network **metrics** (discussed in more detail below) which describe the position of the node in the network (Farine and Whitehead 2015). Links represent the relationship between nodes, usually measuring **association** strength (co-group membership or how close individuals are to each other spatially) or interaction frequency (at what rate individuals interact) (Croft et al. 2008, Farine and Whitehead 2015).

A visual display of a social network sometimes arranges nodes and links so nodes are displayed in some sort of order (alphabetically or numerically) that can be easily referenced. More commonly, nodes are arranged relative to their relationship with each other, with nodes that are connected or more strongly connected to each other positioned closer together (Figure 3.1, Croft et al. 2008).

Sociograms primarily serve to visualise network data and are useful for developing initial hypotheses and for checking results. Most actual analyses of social networks work with the matrix format of social network data. For social networks where the nodes represent individuals and the links represent their relationship, the network is displayed in an N X N matrix, where all the individuals (the nodes) present in the network are the labels of the rows and columns, and each matrix cell represents a relationship (or link) between individuals. The matrix file is referred to as an interaction or association matrix, depending on the relationship described. The matrix file is usually accompanied by an attribute file, which contains the details of the characteristics of interest for each of the nodes of the matrix.

The power of SNA comes from the methods available for assessing network structure through global and node-level network metrics (Krause et al. 2015). Global network metrics are used to describe network level trends such as overall connectedness (Croft et al. 2008, Borgatti et al. 2013). Node-level metrics describe the position of individuals in the network, and, when considered together with individual attributes, can be used to draw conclusions about how individual characteristics may influence the position of an individual in the network and contribute to the formation of overall social structure (Croft et al. 2008). The node-level metrics used in this study are described in detail in section 3.1.2.



a) b)

Figure 3.1. Two examples of social network sociograms. In both sociograms the nodes are arranged so that those that are connected, or more strongly connected, are positioned closer together. The first panel (a) shows a binary undirected network. The second panel (b) shows a weighted directed network. Wider links indicate individuals who are more strongly connected and arrowheads indicate the direction of the connection.

A network can be either **binary** (Figure 3.1a) or **weighted** (Figure 3.1b). In a binary network, all links are based on the presence or absence of a relationship between two individuals and all present links have a weight of one. Weighted networks have links with numeric values that indicate the strength of the relationship between the two nodes of interest (Figure 3.1b). The majority of initial network analyses developed were based on binary networks (Whitehead 2008a), although raw data collected for analysis usually starts as a weighted network (Farine and Whitehead 2015). For example, during data collection animal A and animal B may be seen together in the same group on three occasions, but in the final binary network this relationship is represented by a link with a value of one. Weighted networks can be made binary by applying a threshold to the data, where links above certain values are kept and assigned a value of one, and links below a certain value are discarded (Croft et al. 2008, Farine and Whitehead

2015). As analysis methods for animal social networks have become more refined, thresholding has come to be treated with more caution, as threshold assignments are usually arbitrary and different thresholds can lead to very different conclusions about the structure of the same network (Croft et al. 2008, Farine and Whitehead 2015). Network thresholding has been found to contribute to high rates of both type I and type II error (Langer et al. 2013, Farine 2014, Farine and Whitehead 2015). As a result, performing analyses with weighted, non-thresholded networks and using thresholds for data display rather than for analysis has become the preferred course of action for animal SNA (Franks et al. 2010, Farine and Whitehead 2015). Analysis of weighted networks has become easier in recent years, as more and more methods for calculating network metrics and performing analysis on weighted networks have been developed (Opsahl and Panzarasa 2009, Opsahl et al. 2010, Farine 2014).

Networks can be either **undirected** (Figure 3.1a) or **directed** (Figure 3.1b). In an undirected network the link value from individual A to individual B is the same as that from B to A. In a directed network, there can be a link from A to B, but no link, or a link of a different value, from B to A. Undirected networks can also be described as symmetric, as when displayed in matrix format the link values in the upper half of the matrix (above the diagonal) are identical to the link values in the lower half of the matrix (below the diagonal). Directed networks, in contrast, are asymmetric. By convention, the matrix form of a directed network lists actors (the individuals giving an interaction or from whose perspective the relationship is being described) down the rows of a network matrix, while the receivers of the interaction or relationship are listed across the matrix columns (Croft et al. 2008).

SNA is a very data-hungry method of analysis (Whitehead 2008b). During analysis and the drawing of conclusions, there is always the risk that the lack of a link between two individuals exists not because they never or rarely associated, but simply because the observer was not there when an association or interaction did occur. This source of error can never be eliminated, but with larger datasets it is much more probable that the lack of a link indicates individuals who truly did not interact. Whitehead (2008b) found that for association matrices, which record the proportion of all observations during which two individuals were observed in the same group, bringing the standard error of the predicted association matrix to <0.1 required 15 observations of each associated pair, or **dyad**, and bringing the standard error down to <0.05 required 50 observations. All studies are generally limited in some way by resources or logistics (Farine and Whitehead 2015). In more limited studies, it is better to have a greater number of measures of a few individuals than to have a few measures of many individuals (Franks et al. 2010, Farine and Whitehead 2015).

In the analyses discussed in the following three chapters, networks were either spatial or interaction networks. The **spatial networks** were weighted and undirected association matrices. Each node represented an individual takhi and the links between two takhi represented the median distance between them during the observation season (defined in section 3.2.1.1). The spatial networks thus displayed the average spatial distribution of individual takhi in the focal groups for the observation period of interest. Links with high weights in the spatial networks represented pairs of individuals who were, on average, close to each other across the observation period. The **interaction networks** were weighted and directed interaction matrices. Each node represented an individual takhi and each link represented the rate of interactions (in interactions per hour) given by each actor to each receiver during the observation season. The interaction networks thus showed how all individual takhi were connected by interaction occurrence. Links with high weights in the interaction networks represented pairs of individuals who exchanged interactions at a high frequency during the observation season.

3.1.2. Social network metrics applied, and how each metric informs on social structure.

Of the myriad social network metrics available, six were used in this study; weighted degree, strength, weighted indegree, instrength, weighted betweenness, and weighted clustering coefficient.

3.1.2.1. Degree, strength, indegree, and instrength

Node **degree** simply describes the number of links in a network that are attached to the node of interest. Node **strength** is the summed weight of all links attached to the node of interest. In binary networks, node strength and degree have the same value, as all links have a value of one. Individuals with high node strength or degree are more central to the network, as they are connected to a greater number of individuals and/or have a strong connection to other individuals.

When dealing with weighted networks, degree and strength can be limited in their usefulness, as degree only considers the number of nodes to which the node of interest is connected, while strength only considers the total involvement of the node of interest in the network through the sum of all connected links (Opsahl et al. 2010). Opsahl et al. (2010) proposed another method of calculating degree in weighted networks which incorporates a 'tuning parameter', α, that makes it possible to adjust the importance of the number of links relative to the importance of link weights. Opsahl et al.'s (2010) proposed method of calculated weighted degree is shown in Equation 3.1.,

Equation 3.1 $$C_D^{w\alpha}(i) = k_i \times \left(\frac{s_i}{k_i} \right)^{\alpha}$$

where:

k_i = the count of all links connected to node i

s_i = the sum of the weights of all links connected to node i

α = the tuning parameter.

When $\alpha = 1$, the value calculated is the same as standard node strength. When $\alpha<1$, a greater number of different contacts over which total strength is distributed increases the node's degree score. When $\alpha>1$, a greater number of different contacts over which total strength is distributed decreases the node's degree score (Opsahl et al. 2010).

In this study, metrics were calculated with $\alpha = 1$ (to determine the network strength of each takhi) and $\alpha = 0.5$ (to determine the weighted network degree of each takhi). Individuals with higher strength scores were those who were closer to a few or many other individuals or had initiated a higher rate of interactions overall. Individuals with higher degree scores were those who were closer to more individuals or initiated a higher rate of interactions toward a greater number of other individuals (Opsahl et al. 2010).

In directed networks such as interaction networks, 'degree' and 'strength' become synonymous with '**outdegree**' and '**outstrength**.' When outstrength and outdegree are calculated, only links that originate at the node of interest are considered. For example, in a directed network, if takhi A gave one head threat to takhi B and two head threats to takhi C and received two head threats from takhi D, her strength would be three, NOT five. **Instrength** and **indegree** describe the number and value of links that terminate at the node of interest, thus, the number of interactions received by the individual. In the previous example, takhi A's instrength would be two.

3.1.2.2. Betweenness

In a binary network, **betweenness**, sometimes called node betweenness, measures the number of shortest paths between all other nodes in the network that pass through the node of interest (Croft et al. 2008). Thus, betweenness is a measure of how important an individual is in connecting the other members of a network. A shortest path in a network is the minimum number of steps (moving from node to node) required to reach individual B from individual A. If A is directly connected to B, the shortest path is 1. Freeman (1979) defined betweenness using Equation 3.2,

Equation 3.4 $$C_B(i) = \frac{g_{jk}(i)}{g_{jk}}$$

where:
g_{jk} = the number of shortest paths between nodes j and k
$g_{jk}(i)$ = the number of shortest paths between nodes j and k that go through node i.

Opsahl et al. (2010) developed a method of calculating weighted betweenness that could be applied to a non-binary network. The weighted betweenness formula accounts for both the number of intermediary nodes in the network and the weight of the links connecting nodes. Opsahl et al. (2010) developed a shortest path formula (Equation 3.3) based on previous work with weighted networks by Dijkstra (1959), Brandes (2001), and Newman (2001).

Equation 3.7 $$d^{w\alpha}(i,j) = \min\left(\frac{1}{(w_{ih})^{\alpha}} + \ldots + \frac{1}{(w_{hj})^{\alpha}}\right)$$

Where:
w_{ih} = weight of the link between individual i and some intermediary individual h
w_{hj} = weight of the link between some intermediary individual h and the destination individual j
α = a tuning parameter. $\alpha < 1$ gives preference to shorter paths with weak links and $\alpha > 1$ gives preference to longer paths with strong links.

Essentially, the formula finds the shortest path with the least resistance between two nodes in the weighted network by summing the inverse of the link between all nodes along all possible paths and looking for the lowest value. By taking the inverse of the weighted link, individuals with a higher weight to their link offer a shorter and less resistant path than individuals with a lower weight to their link (Opsahl et al. 2010). The tuning parameter makes it possible to adjust the betweenness calculations to give greater preference to a shorter path with weaker ties (if $\alpha<1$) or a longer path with stronger ties (if $\alpha>1$). In this study, the α tuning parameter was set to 1.5. Thus, when finding a shortest path, individuals who interacted more frequently (or were closer together) were preferred to individuals that interacted less frequently (or were further apart) as potential shortest paths (Opsahl et al. 2010). The formula for weighted betweenness centrality developed by Opsahl et al. (2010) and used in this study is shown in Equation 3.4,

Equation 3.10 $$C^{w\alpha}_{B}(i) = \frac{g^{w\alpha}_{jk}(i)}{g^{w\alpha}_{jk}}$$

where:

$g^{w\alpha}_{jk}$ = the number of shortest weighted paths between nodes *j* and *k*
$g^{w\alpha}_{jk}(i)$ = the number of shortest weighted paths between nodes *j* and *k* that go through node *i*

In directed networks such as interaction networks, possible shortest paths are restricted to the direction of the network links (Opsahl et al. 2010). For example, if takhi A gave a head threat to takhi B and takhi C, and takhi B gave a head threat to takhi D while takhi C received a head threat from takhi D, a shortest path from takhi A to takhi D could travel from takhi A to takhi B to takhi D, but could never travel from takhi A to takhi C to takhi D, because direction of the last link is from takhi D to takhi C, rather than from takhi C to takhi D. In this study all interaction networks were symmetrised prior to calculating betweenness values to create an undirected network, so that the importance of an individual as a connector was not dependent on whether they were giving or receiving interactions. Networks were symmetrised by calculating the sum of the weight of the links between two individuals. For example, if in the original directed network takhi A gave takhi B two head threats and takhi B gave takhi A three head threats, in the symmetrised network, the link value between takhi A and takhi B *and* between takhi B and takhi A would be five.

Individuals with the highest spatial betweenness are often those positioned at the boundary between two social groups. Individuals with high betweenness in social networks are not necessarily the most socially active, but their position is such that their presence may connect social subgroups that otherwise would be completely separated. Individuals with high betweenness are often considered key 'brokers' in the flow of information and the transmission of disease or parasites (Corner et al. 2003, Croft et al. 2008, Krause et al. 2015). Lusseau and Newman (2004) suggested that individuals with high betweenness may provide important "social glue" connecting individuals from smaller groups into a larger community, and thus helping to maintain social cohesion. However, Whitehead (2008a) suggested that a more parsimonious explanation would be that individuals with high betweenness were more often young dispersers or other individuals on the periphery of established groups who would consequently more often serve as a bridge connecting separate social subgroups. This study is interested in individuals with high betweenness as they create a bridge between otherwise disparate social groups, and thus could serve as important promoters of cohesion. The identity and characteristics of the individuals with high betweenness will inform whether individuals with high betweenness in equid societies appear to be brokers in the manner of Lusseau and Newman (2004) or more a juvenile fringe element, in the manner of Whitehead (2008a).

3.1.2.3. Clustering coefficient

The **clustering coefficient** (or cluster value or local clustering coefficient) of a node in a binary network measures the extent to which the immediate associates (or **neighbours**) of an individual are themselves associated (Whitehead 2008a). Individuals with high clustering coefficients are generally part of a closely interconnected subgroup while individuals with a lower clustering coefficient are often more socially peripheral (Whitehead 2008a). The clustering coefficient is defined as the number of closed **triplets** (where the two neighbours of node *i* are also connected to each other) divided by the total number of closed and open triplets (where *i* is connected to two neighbours who may or may not be connected to each other) (Opsahl and Panzarasa 2009). Open triplets are those where the two neighbours of *i* are NOT also connected to each other. The clustering coefficient is most easily calculated by Equation 3.5, from Croft et al. (2008),

Equation 3.13

$$C_i = \frac{2t_i}{k_i(k_i-1)}$$

where:

t_i = the number of closed triplets of which node *i* is a part.

k_i = the number of nodes a distance of one link from *i*.

Barrat et al. (2004) developed a method for calculating clustering coefficients in a weighted network. The weighted clustering coefficient of node *i* is found by calculating the arithmetic mean of the link weights of all closed triplets centred on *i* to obtain a '**triplet value**' for each closed triplet. The sum of all closed triplet values centred on *i* is divided by the sum of all triplet values (open and closed) centred on *i*, (Barrat et al. 2004, Opsahl and Panzarasa 2009), as is shown in Equation 3.6,

Equation 3.16

$$C_w = \frac{\sum_{\tau_\Delta} w}{\sum_{\tau} w}$$

where:

$\sum_{\tau_\Delta} w$ = the summed values of closed triplets centred on the node of interest

$\sum_{\tau} w$ = the summed values of all triplets centred on the node of interest.

Currently, weighted local clustering coefficients have only been defined for undirected networks, so, as with betweenness, all interaction networks were symmetrised before calculating clustering coefficients.

3.1.3. Summary of network metrics considered

All the network metrics described above are node-level measures of network centrality. However, each metric provides a slightly different perspective on the position and importance of individuals in the network. Table 3.1 presents a summary of network metrics, what they measure, and how high scores can be interpreted.

Table 3.1. A summary of how the network metrics applied in this study can be interpreted in the context of spatial and interaction networks.

Network metric	Measures…	Individuals with a high score…
Strength	…the strength of connections (or of given connections, for directed networks).	…are very close to, or give many interactions to, a few or many individuals.
Degree	…the number *and* strength of connections (or of given connections, for directed networks).	…are very close to, or give many interactions to, many individuals, but will have an even higher score if the connections are strong.
Instrength	…the strength of received connection.	…receive many interactions.
Indegree	…the number *and* strength of received connections.	…receive interactions from many individuals, but will have an even higher score if they receive many interactions.
Betweenness	…the individual's importance as a connection broker.	…are the bridge connecting many individuals either spatially or through interactions.
Clustering coefficient	…the number and strength of well connected neighbours.	…are close to many neighbours that are also close to each other, or interact with individuals who also interact with each other.

3.1.4. Methods of hypothesis testing in social networks

Tests for significant differences in observed network metrics among individuals cannot be performed using standard statistical tests, as social networks inherently violate several of the basic assumptions of standard interferential tests (Croft et al. 2011, Borgatti et al. 2013, Farine and Whitehead 2015). Standard statistical tests assume that all observations are independent and that the data represent a random but descriptive sample of the population. In a spatial or interaction matrix, in each row the receivers of the links are all connected to the same actor, and so are not independent. If that actor has a particularly extreme attribute score, the links to all connected receivers are affected (Borgatti et al. 2013, Farine and Whitehead 2015). In addition, social network data do not generally represent a random sample. More often the data represent a deliberately selected subset of the population or even include the whole population (Borgatti et al. 2013).

A common method for detecting significance in network structure is to compare the observed network to a null model in the form of a random network, often built from random permutations of the observed network (Croft et al. 2008, Farine and Whitehead 2015). From comparison with many random networks, it is then possible to determine whether the structure of the observed network is significantly different from what might be expected to be found in a network made up of random associations within the population of interest (Farine 2014, Farine and Whitehead 2015).

3.1.1.1. Different methods of network permutation

Permutations of observed data are preferred for hypothesis testing, as permutations of observed data are more apt to maintain a general network structure similar to the observed network in terms of global network characteristics such as link density (how many links are present) and degree distribution (how many individuals have higher versus lower degree scores) (Opsahl et al. 2008). A common approach for creating null model networks from observed data is node-based permutation (Farine and Whitehead 2015). A less commonly applied method is link-based permutation (Opsahl et al. 2008, Farine 2017).

3.1.1.1.1. Node-based permutations

Node permutations are the simplest and most widely used method of network permutation (Farine 2017). Node permutations re-shuffle the attributes of the nodes in the network, essentially randomly relabelling all network nodes. As a result, while the permuted network will still have the same number of females as the observed network, the females will be assigned different links than they had in the observed network. Node permutations cannot control for network parameters other than the number of individuals of each attribute type (Farine and Whitehead 2015) and are best used when the observed network links are believed to be a fairly accurate representation of true network structure (Croft et al. 2011). When node permutations are used, the randomisation of the network allows the formation of new links connecting individuals that had no connections to other individuals in the original network.

3.1.1.1.2. Link-based permutations

Link-based permutation methods are currently much less common in animal SNA than are node permutation methods (Farine 2017), but can be better than node permutations at maintaining the overall topology of the network (Opsahl et al. 2008).

3.1.1.1.2.1. Link permutations

The link reshuffling permutation repeatedly randomly selects two links and swaps their destinations (Opsahl et al. 2008). For example, takhi A was linked to takhi B and takhi C was linked to takhi D in the original network, but following permutations takhi A became linked to takhi D, and takhi C became linked to takhi B. The link permutation method maintains the outstrength but not the instrength of each node in the network (Opsahl et al. 2008). The link permutation method is more conservative than the node permutation method in terms of maintaining original network structure, but more liberal than the weight permutation method.

3.1.1.1.2.2. Weight permutations

The network link weight reshuffling permutation is another link-based method which randomly moves link weights around the network (Opsahl et al. 2008). This creates a random network, but maintains the distribution of link values and does not add any links between individuals where there were no links in the original network (Opsahl et al. 2008). In addition, the number of links originating from any one node is not changed. The weight permutation method is the most conservative of the three permutation methods described here.

3.1.1.2. Testing for a significant difference in network metrics

To test for a significant difference in network metrics among individuals with differing attributes (for instance, individuals of differing reproductive state), a test statistic is chosen and calculated for the observed network (Whitehead 2008a). The observed test statistic is compared to a series of test statistics calculated for many randomly permuted networks based on the original data. For example, to test for a significant difference in node strength among individuals of differing personality type, a Kruskal-Wallis test can be used to generate an H statistic for the observed network, which is compared to a series of H statistics generated from 1000 randomly permuted networks. Each network permutation starts with the observed network, rather than working from a network already permutated once, making them independent from each other. Usually at least 1000 independent permutations is sufficient for determining if the observed network is significantly different from random (Whitehead 2008a, Ramos-Fernandez et al. 2009, Farine 2014, Farine and Whitehead 2015). For a two-sided null hypothesis test, if the absolute value of the test statistic is greater than 95% of the absolute values of the test statistics obtained from the permuted networks, the individuals with different attributes in the observed network can be considered to have significantly larger or smaller metric scores than would be expected by chance (Whitehead 2008a). For the node strength example, if the observed H statistic is greater than 95% of the randomly generated network H statistics, it can be concluded that there is a greater difference in the distribution of strength scores among individuals with different personality types than would be expected if links between individuals in the network occurred randomly.

3.2. Applied SNA methodology

3.2.1. Data collection for SNA

3.2.1.1. Data collection periods and focal groups

Feh et al. (2001)'s definition of a group was applied for this study, where a group was a collection of animals whose group diameter was less than the distance between groups AND members showed coordinated movements across multiple hours. Family groups were those that met the group definition and consisted of a mature stallion and one to several mares. No multi-stallion families occurred at either study site.

Data at Seer were collected across three study periods; October 11 – November 30, 2014, March 13 – April 26, 2015, and June 14 – July 13, 2015. Across all three study periods, two hours, or sometimes three in summer, of observation were conducted per day. Spatial and interaction data were collected simultaneously. Spatial data were collected on all takhi within range during the observation, while interaction observations switched between focal family groups after each hour. Interactions were only recorded if they involved at least one focal group member. Observation times alternated between morning and evening, beginning approximately an hour after sunrise in the morning, and approximately an hour before sunset in the evening, when the takhi were the most active (C. Feh, pers. comm. 2014). The actual time of the observation varied depending on the time of year, but most observations occurred between 10:00 and 12:00 and between 16:00 and 18:00 (see Figure 3.2).

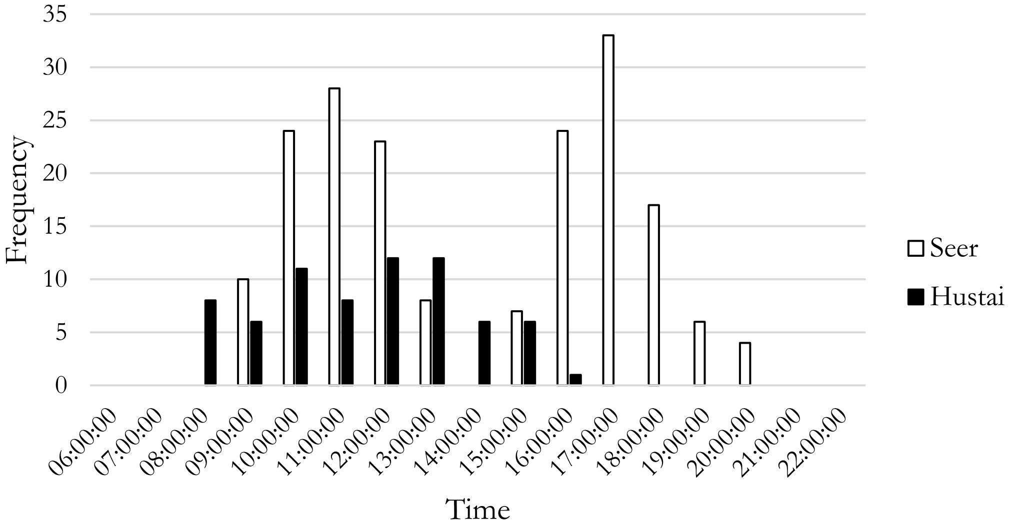


Figure 3.2. The frequency distribution of simultaneous observation start times at Seer and Hustai.

At the time that data collection began (October 11, 2014) the Seer takhi population consisted of 43 takhi living in three family groups and one additional maverick mare, BG. By the end of data collection, the population had increased to 53 individuals and four older juveniles had left their family groups to join BG. One colt (TO) had also left the family groups and was living on his own. One mare (LI) was removed from the herd in May of 2015, prior to the birth of her foal. Individuals who were not members of the three main family groups were classified in the group category 'OTHER'. Family groups were named with the ID of the stallion and the suffix 'G' for 'group'. Appendix 3.II, Table 3.II.1 shows the individuals in each family group, as well as their reproductive state and assessed personality type. The three Seer families, 'BRG', 'CRG', and 'DIG', often travelled together and rested in close proximity (<150 m). The families would occasionally separate and travel independently, but usually rejoined into a larger herd within two or three days. BG and the dispersing juveniles who joined her were rarely observed to come in contact with the three family groups. When they did, they were usually driven off by one or another of the family stallions.

Data at Hustai were collected across four study periods; September 4 – September 11, 2014, January 25 – February 1, 2015, May 5 – May 9, 2015, and July 25 – July 30, 2015. Observations at Hustai generally followed the same methodology as used at Seer. However, due to logistical and financial restrictions, fewer data were collected over shorter time periods in each season. Hustai's terrain and larger takhi population made relocating individual groups challenging, so one focal group was followed per day for seven hours, with the first observation beginning within an hour of sunrise. The start time of observations was therefore fairly evenly distributed between 08:00 and 16:00 (Figure 3.2). During the seven hours, observations were alternated between recording one hour of simultaneous observations (recording interactions and spatial distribution) and one hour of behaviour scan samples for personality assessment (see Chapter 2).

A combination of population size, with 318 individuals and 33 family groups (Usukhjargal 2014), and study restrictions made it impossible to observe all family groups at Hustai. Hustai focal family groups were selected with the aim of choosing established family groups whose home ranges included the central Bayan Valley (see Figure 3.6a). Established family groups were those that were considered by the Hustai rangers to be relatively stable in membership and consistent in space use. Five focal groups were selected, 'BDG', 'DNG', 'KEG', 'WNG', and 'ZRG'. Appendix 3.II, Table 3.II.2 lists the individuals in each family group, as well as their reproductive state.

Observations at both Seer and Hustai were split into two study periods, 'Non-breeding' and 'Breeding.' The gestation period of takhi is the same as that of other *Equus ferus spp.*, approximately 11 months, so the breeding season is roughly equivalent to the foaling season

(Ransom et al. 2016). The first foal at Seer was born on April 17th, 2015, so for this study the end of March was the cut-off between the breeding and non-breeding seasons at both study sites. The non-breeding period at Seer included data collected from October, 2014 through March 31, 2015. The breeding period included data collected from April through July 13, 2015. The non-breeding period at Hustai included data collected between September, 2014 and February, 2015. The breeding period included data collected from May to July, 2015.

3.2.1.2. Collecting spatial data

3.2.1.2.1. Developing methodology for spatial measurements

The relative cohesion and spatial distribution of herds and family groups at Seer and Hustai was estimated by measuring the spatial distribution of individual takhi over time. A vector rangefinder (TruPulse 360R model; Laser Technology, Inc., Centennial, CO, USA) was used to measure the spatial distribution of individuals. A series of trials were conducted with the rangefinder to assess its accuracy and precision when measuring the spatial distribution of the takhi herds. Initial pilot tests indicated that the presence of ferrous metals, including the voice recorder necessary to record all measurements for later transcription, could influence the rangefinder's bearing calculations. All measurements were therefore recorded using a headset with a microphone, allowing the spatial measurements observer to keep the metal in the voice recorder from influencing the rangefinder's angle measurements. The rangefinder was mounted on a carbon-fibre monopod to improve stability during measurements.

3.2.1.2.1.1. Missing line error estimates

The aim, when measuring the spatial distribution of the takhi, was to create a model of the position of all takhi present relative to each other. As individuals rarely remained stationary during the spatial distribution measurements, the final spatial measurements were sure to contain some error in the positioning of individual takhi. This error could not be eliminated with the equipment available, but could be minimised. Measuring all takhi present in the Seer herd (40 to 50 individuals) required seven to 11 minutes. Measuring the position of each takhi relative to the observer would have required that the observer remain in the same position for the entire measurement period or that the observer re-record their new GPS position every time they moved during the measurement session. The terrain at both Seer and Hustai consisted of areas of low rolling hills and more rugged mountainous areas. Therefore, it was often necessary for the observer to change location multiple times during the measurement session to obtain measurements for all takhi present. Use of the rangefinder's missing line measurement function made it possible to record the observer's GPS location, measure the angle and bearing to a starting takhi, and then measure the distance and bearing between takhi, thus eliminating the need to re-record the observer's position if they moved to follow the takhi during the measurement period (Figure 3.3).

Figure 3.3. Demonstrating the use of the rangefinder missing line function. The yellow lines mark the measurements taken by the rangefinder and the red line represents the missing line length and bearing calculated by the rangefinder.

The variation in measurement results using the missing line function was tested by repeatedly measuring the distance between two takhi and checking for variation in both the distance and bearing of the calculated missing line. Missing line bearing measures showed much more variation than did distance measures. The average standard deviation in bearing for the missing line between moving takhi was 6.48 ° (Table 3.2). The maximum standard deviation for a dyad was 14.37 °, with four measurements. The average standard deviation of measurement for the bearing between standing takhi was 2.38 °, while the maximum was 5.3 ° with 16 measurements of low quality targets.

Table 3.2. Average standard deviation of missing line distance and bearing measurements between two takhi, moving at a walk and standing still.

	Bearing *Average ST Dev*	Distance *Average ST Dev*
Moving	6.48	1.63
Standing	2.38	0.45

The average standard deviation of missing line distance measures to a moving takhi was 1.63 metres (Table 3.2), with a maximum standard deviation of 5.22 metres with seven measurements for one dyad. The average standard deviation of distance to a standing takhi was 0.45 metres, while the maximum standard deviation was 0.75 metres with 18 measurements. Although not perfect, the missing line function of the rangefinder was determined to be sufficient for recording the location of all takhi present during the measurement interval.

3.2.1.2.2. Final methodology for spatial measurements

The methodology for conducting spatial distribution measures was the same for both Seer and Hustai and proceeded as follows.

The observers recording takhi spatial distribution and takhi interactions began their observations at the same time. At the beginning and end of the observation hour the spatial distribution observer would also record the temperature (ºC) and wind speed (m/s) using a Kestrel 3000 Wind Meter (Nielsen-Kellerman Co., Birmingham, MI, USA). The spatial observer would repeat the measure of the locations of all takhi within range at 15-minute intervals during the hour-long observation of each focal group, for a total of five measurements per individual takhi per hour of observation.

For each spatial measurement session, the spatial observer would select a location from which it was possible to see the majority of takhi, and then record her (the observer's) GPS position. The observer would next measure the distance and bearing from her position to a starting takhi. The observer would then use the missing line function of the rangefinder to measure the distance and bearing from the starting takhi to a second takhi, second takhi to third takhi, and so on, until the locations of all takhi present were measured.

Allowing for some variation due to terrain, the distance cut-off for measuring all individual locations in widely spread family groups was ~400 m. If the groups were more widely spread, there was no time during the 15-minute interval between measurements for the observer to move between groups. In those cases, the spatial observer would only measure the interindividual distances of members of the interaction observer's focal group until other family groups moved within 400 m of the focal family. It was sometimes possible to obtain rough locations on groups from 400 up to 1000 m away, but at >400 m it was not possible to measure and identify individuals. For groups at distances of >400 m, the observer would record the distance and angle to the geometric centre of the group. If possible, depending on target quality, they would also measure the width of the family groups (takhi at four directional extremes of the group structure, identifying individuals) and the location of the stallion (if visible). At the end of the observation period, the observer would move closer to the out-of-range takhi, and record the location of all individuals.

If the spatial observer needed to change position in the middle of a recording session and after shifting position, all previously measured takhi were out of sight (behind some visual barrier such as a rocky outcrop), the observer would record a new GPS position. Otherwise, from the new position the observer would record the distance from a previously measured takhi to the takhi now in view.

When measuring the distance between takhi dyads, the observer would record the name and basic activity (or behaviour state) of each takhi and the part of their body that was at the centre of the rangefinder cross-hairs. Basic activities included grazing, walking, other movement, resting standing, resting sternal, resting lateral, vigilant, and other. Parts of the body measured included head, neck, withers, front shoulder, shoulder, barrel, rump, back, and leg. Preferentially the observer would measure the shoulder, barrel, or rump, as these provided the best targets for the rangefinder, but if those parts of the takhi were obscured by landscape or other individuals, lower quality targets were used.

If it was not possible to measure all takhi because they were too active (rapidly changing position within the group due to the presence of insects or, as a group, moving at a fast walk or trot to another location) the spatial observer would measure the width of the family groups (takhi at four extremes of the group, identifying individuals), and the location of the stallion (if visible), as stallions often had very different movement patterns relative to the rest of the family group. At the beginning of the next 15-minute interval, the observer would return to the original methodology. If group activity had not decreased, the observer would continue to use the secondary measuring method.

3.2.1.3. Interaction observations

Several methods of recording interactions were tested, both prior to leaving for the field and following arrival at the primary research site in Seer. Initially, attempts were made to film each complete observation session so as to have a video record of all interactions occurring between takhi. However, through successive trials with the Park Hill horses at Brackenhurst Campus at NTU, the rescue herds at Bransby Horses, Bransby, UK, and the herd at Seer, it became clear that filming all takhi for the full observation was not logistically feasible.

Researchers at Seer have been recording interindividual interactions since 1993 and have an established ethogram incorporating all major interactions. Seer rangers were trained in recording those interactions during daily observation sessions, and observer agreement was estimated from joint observations on usually a bi-monthly basis (see section 3.2.1.3.1). The Seer ethogram incorporated all interactions with a strong influence on takhi spatial distribution, so ranger-recorded data were used for all Seer observations (the ethogram used is shown in Appendix 3.III). Following each day of observations, all data for each observation were consolidated into a master file for later processing and analysis. All interaction observations followed the established Seer methodology, which used focal group sampling (Altmann 1974). The interaction observer followed one focal group for the first hour and switched to another group for the second hour of observation. At the beginning of each hour of observation, the observer recorded the time, date, and GPS location of the focal family group. During the observation, the interaction observer recorded all ethogram interactions (both intra- and intergroup) that involved at least one member of the focal group.

Rangers at Hustai did not conduct behaviour observations as the rangers at Seer did, so both spatial observations and interindividual interactions were recorded by one observer. During the spatial distribution measures at the 15-minute intervals (described above in section 3.2.1.2.2.), a field assistant recorded videos of the full focal group to capture any interactions that occurred while spatial measurements were being taken. On returning to base camp at the end of the observation period, all videos made during the spatial measurement periods were reviewed and interactions occurring during that time were added to the interaction observation file.

All observations for both Seer and Hustai were transcribed from voice files into spreadsheet format, with one spreadsheet per observation. Each spreadsheet also included all interactions recorded during the observation.

3.2.1.3.1. Tests for interaction observer agreement at Seer

At Seer, interactions were categorised as either quantitative or non-quantitative. Based on the Seer ethogram, every occurrence of a quantitative interaction was recorded, but non-quantitative interactions were to be recorded opportunistically and with lower priority than quantitative interactions.

The interactions incorporated in SNA (discussed in more detail in section 3.2.3.2.1) included one technically non-quantitative interaction; head threats (see Appendix 3.III for definitions). During field work, categorisation as quantitative or not quantitative did not appear to influence recording frequency and both were included in observer agreement reports. A breakdown of overall observer agreement during July for multiple-observer observations showed levels of disagreement ranging from 29 to 100% (Table 3.3). Head threats (a non-quantitative interaction) had the highest agreement of all interactions included. Mutual grooming had a higher percent disagreement, but also much lower occurrence, than head threats.

Table 3.3. Breakdown of observer disagreement (n = 3 observers) by interaction for July, 2015. Interactions in bold are listed in the Seer ethogram as non-quantitative. 'All observer combined interactions' show the maximum number of interactions observed during the observation session, whether they were observed by all observers or just one or two. The 'All observed combined differences' column counts the number of interaction occurrences missed by at least one observer. The '% observer combined difference' lists the percent of total interaction occurrences recorded that were missed by at least one observer.

Interaction name	All observer combined interactions	All observer combined differences	% observer combined difference
charge	2	2	100
chase	2	1	50
mutual groom	5	2	40
play bite	2	2	100
play rear	0	0	*NA*
play chase	0	0	*NA*
play kick	2	2	100
head threat	**68**	**20**	**29**

Looking at observer agreement across the period of data collection (October, 2014 to July, 2015), overall % difference in observation frequency ranged from 6.3% to 53% (Table 3.4). However, non-quantitative interactions did not appear to be more prone to disagreement than quantitative interactions.

Table 3.4. Overall observer disagreement (% difference in number of all interactions, focal and non-focal, observed/recorded) of observed quantitative and non-quantitative interactions during the study period (October, 2014 to July, 2015) at Seer.

Month	Quant(Q)/NonQuant (N)	# of observers	% difference
October, 2014	Q	2	11.6
October, 2014	N	2	6.3
April, 2015	Q	3	14.6
April, 2015	N	3	16.4
May, 2015	Q	3	14.6
May, 2015	N	3	16.4
June, 2015	Q	2	9.0
June, 2015	N	2	42.0
July, 2015	Q	2	29.0
July, 2015	N	2	47.0
July, 2015	Q	2	42.0
July, 2015	N	2	27.0
July, 2015	Q	2	34.0
July, 2015	N	2	53.0

At Hustai, all interactions were recorded as they were observed, with no breakdown into categories of quantitative or non-quantitative. Only one observer recorded interaction data at Hustai, so observer agreement was not calculated for those observations.

The discrepancies in observer agreement at Seer did not appear to be influenced by the categorization of interactions as quantitative or non-quantitative. Data at Hustai were recorded as observed, with no set priority for different interaction types. Overall, while the low agreement of observers at Seer is cause for caution in ultimate interpretation of results, agreement appeared consistent across all interaction types. Further discussion of the potential consequences of low ranger agreement can be found in Chapter 7, section 7.3.2.

3.2.2. Summary of raw data collected at Seer and Hustai

A total of 184 hours of simultaneous observations were recorded at Seer, including both spatial distribution and interactions (Table 3.5). There were more hours of observation for BRG, CRG, and DIG groups than for the YO/BG group in the OTHER category because the YO/BG group was not formed until May of 2015 (Table 3.5).

Table 3.5. Breakdown by focal group of total hours of simultaneous observation (spatial and interaction measurements) conducted at Seer and Hustai.

Location	Focal group	Hours observed
Seer	BRG	56
	CRG	57
	DIG	55
	OTHER	16
Seer subtotal		184
Hustai	BDG	14
	DNG	10
	KEG	14
	WNG	14
	ZRG	14
Hustai subtotal		66
Total hours of observation		**250**

A total of 66 hours of simultaneous observations were completed at Hustai (Table 3.5). The DNG group was added as a focal group in January, 2015 when two of the original focal groups from September, 2014 could not be relocated. DNG therefore has fewer observations than the other four focal groups.

3.2.3. Data processing for SNA

3.2.3.1. Spatial data

3.2.3.1.1. Creating spatial maps from transcribed rangefinder measurements

As soon as possible following data collection, all recorded spatial distribution measurements were transcribed to a spreadsheet, re-listening to the recordings to double check for accuracy in transcribing individual names and numbers. Measures of distance and bearing were used to calculate the position in space of each takhi. First, the observer's starting GPS location was converted from a WGS 84 to a UTM 46N projection for Seer data and to a UTM 48N projection for Hustai data. All angle measurements were converted from degrees to radians. Then, starting with the latitude and longitude of the observer's position, the distance and bearing to the starting takhi was calculated using Equation 3.7. Then the latitude and longitude of the first takhi, along with the distance and bearing to the second takhi, were used to calculate the position of the third takhi, and so on. All latitude and longitude conversions were performed in an Excel® worksheet.

Equation 3.19 $Lat2 = \cos(a) * d + Lat1 \qquad Long2 = \sin(a) * d + Long1$

Where:

$Lat1$ = The latitude of the observer or of takhi A
$Long1$ = The longitude of the observer or of takhi A
a = the angle, from true north, from the observer to takhi B or takhi A to takhi B
d = the distance between the observer and takhi B, or between takhi A and takhi B
$Lat2$ = the latitude of takhi B
$Long2$ = the longitude of takhi B

Once the latitude and longitude of each takhi was calculated for each interval of the observation, the individual takhi locations were moved into ArcGIS 10.3 (ESRI 2017) using the 'Project XY' tool. The resulting feature classes showed the estimated position of all individuals at each interval during each observation period. Figure 3.4 shows the progressive movement across the hour of all takhi present (the BRG, CRG, and DIG family groups) during observation of interactions involving members of the BRG family group on November 13th, 2014. Figure 3.5 shows all individual takhi locations recorded at Seer during non-breeding and breeding seasons. Figure 3.6 shows all individual takhi locations recorded at Hustai during non-breeding and breeding seasons.

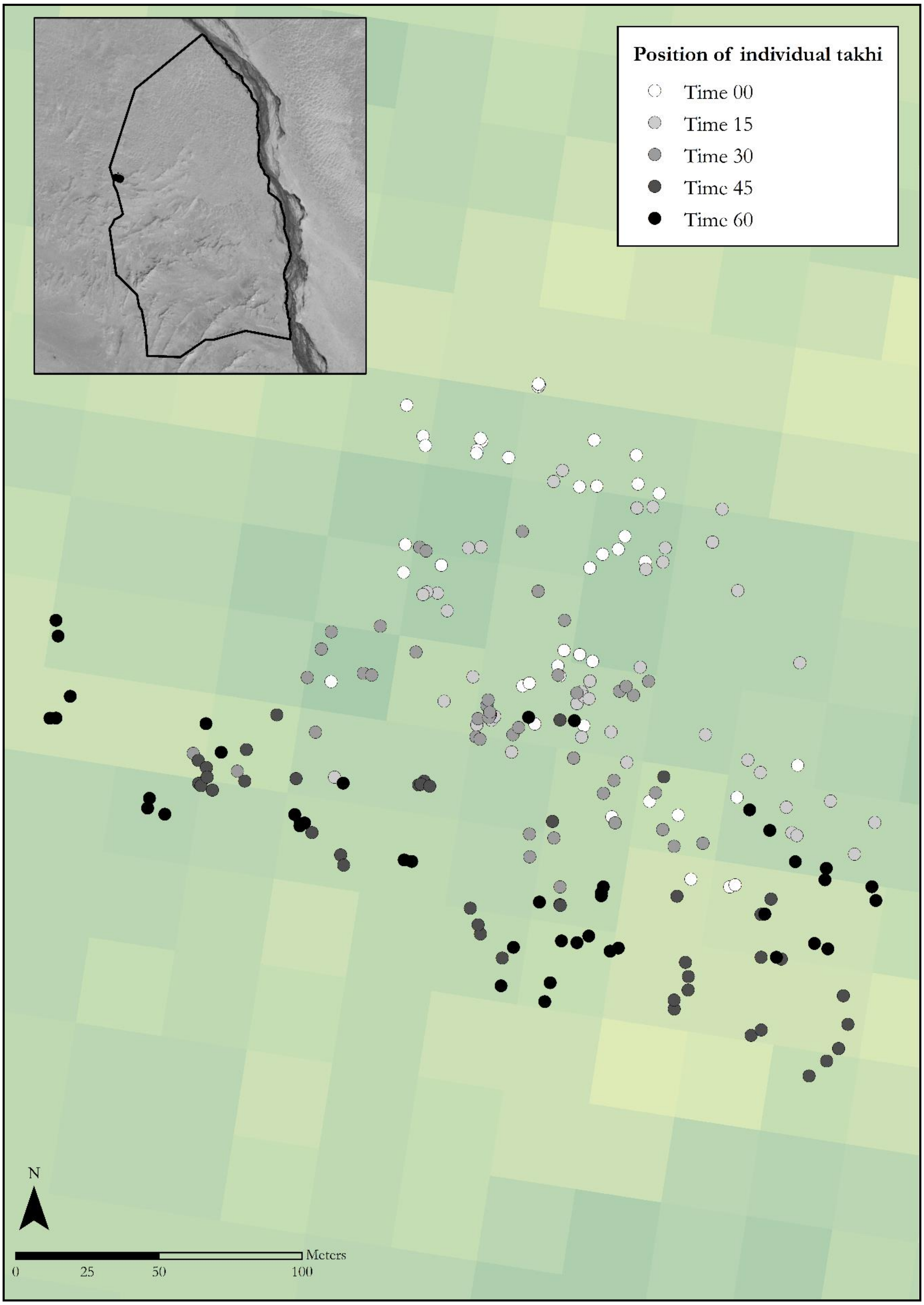


Figure 3.4. The progressive movement of the Seer family groups during one hour of interaction and spatial distribution recording on November 13th, 2014. The map inset shows the position of the family groups within the reserve.

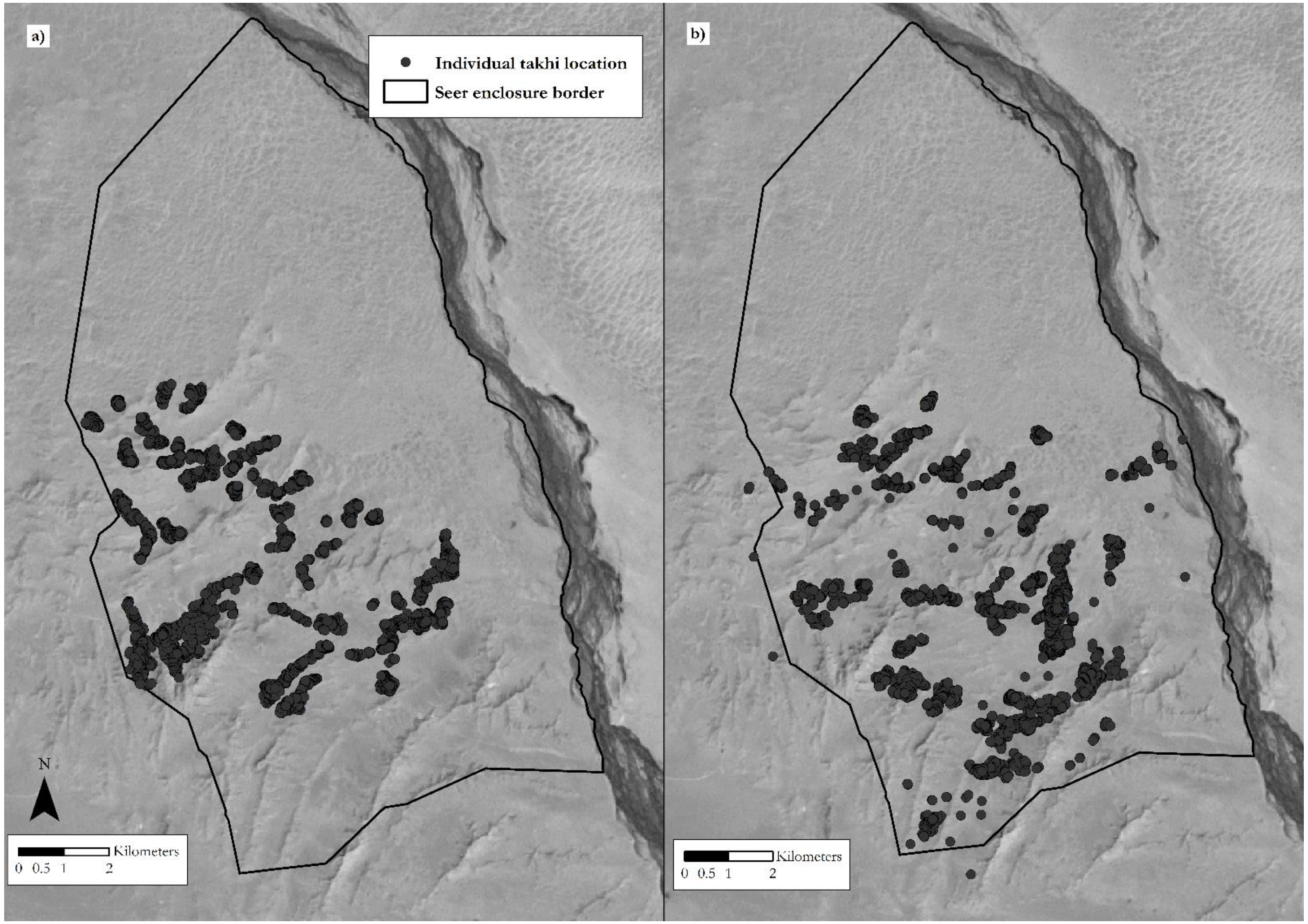


Figure 3.5. All individual takhi locations recorded in the (a) non-breeding and (b) breeding season at Seer.

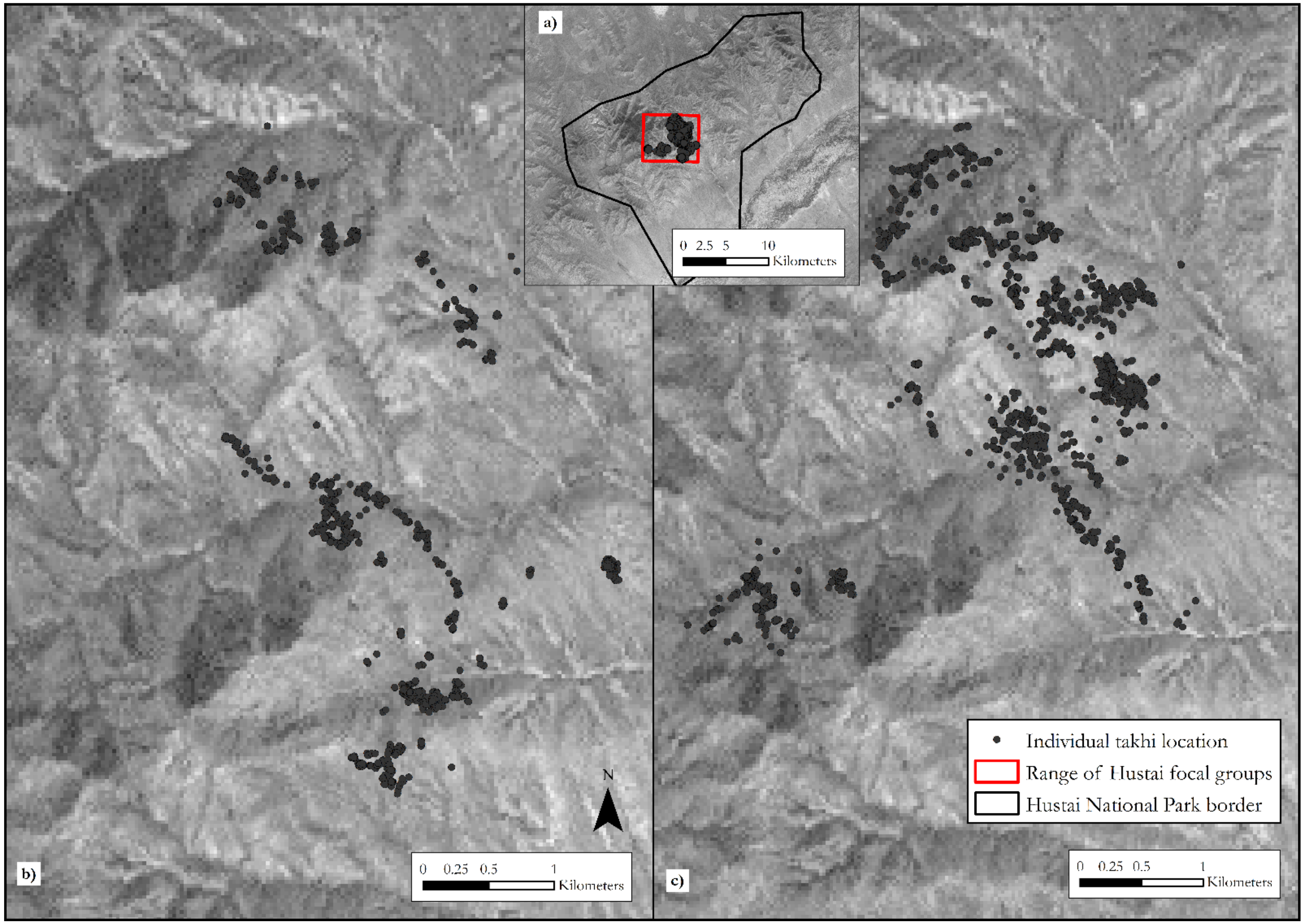


Figure 3.6. Focal family groups at Hustai restricted their movement to hills and valleys around the Bayan Am springs at the centre of the park (a). Maps show the location of all individual takhi locations during the (b) non-breeding and (c) breeding season at Hustai.

3.2.3.1.2. Calculating interindividual distances

The 'point.distance' function in GME (Geospatial Modelling Environment, Beyer 2015) was used to calculate the distance between all possible takhi dyads during each 15 minute interval of each hour of observation. Interindividual distance measurements were then exported to the project database for conversion into spatial networks.

3.2.3.1.3. Creating summarised spatial median networks

Spatial networks were created by calculating the median distance between all present takhi dyads for the observation period of interest. Median distance was calculated because the distribution of interindividual distance measures between each dyad was generally non-normal. To create the median distance networks, first the median interindividual distance across each hour of observation between each dyad was calculated. This first summarization was conducted because, across each hour, depending on how active individuals were during the observation, the distance between takhi A and takhi B during the first measurement was not always independent of the distance between takhi A and takhi B during the second measurement. For instance, the two individuals may have been resting close together for >15 minutes or gradually moving further apart while grazing. Calculating the median distance between individuals across the hour from five measurements in total removed the chance of dependence between interindividual measurements. To obtain the overall median interindividual distance among all dyads across the observation season for the final spatial networks, the median of the median per hour distance was calculated for each season. In the original network of median distance values, higher values indicated takhi who were farther apart, while lower values indicated takhi who were closer together. The weighted metric calculations described in section 3.1.2 were designed with the assumption that higher link weights indicated stronger ties. To meet this assumption, the inverse of all distance measures was calculated, so that higher values in the spatial network indicated takhi who were closer together.

3.2.3.2. Interaction data

3.2.3.2.1. Selecting focal interactions

Interactions included in network analysis were limited to those that were unambiguously agonistic or affiliative (see Chapter 1, sections 1.8.1 and 1.8.2). Agonistic interaction networks included charge, chase, and head threat interactions (Figure 3.7; see Appendix 3.III for ethogram definitions). Affiliative interaction networks included play and mutual grooming interactions (Figure 3.8; see Appendix 3.III for ethogram definitions).

Figure 3.7. Examples of the three interactions included in the agonistic interaction networks; (a) chase, (b) charge, and (c) head threat.

Figure 3.8. Examples of the two interactions included in the affiliative interaction networks; (a) play and (b) mutual grooming.

3.2.3.2.2. Creating intragroup and intergroup networks

All spatial, agonistic, and affiliative networks were split into intragroup and intergroup networks. Intragroup networks only included distance measures or interaction links occurring between members of the same group, and intergroup networks only included distance measure or interaction links occurring between members of different groups. All networks were created as N X N matrices of all takhi present. Links in the spatial networks represented the inverse of the median of the median per observation hour distance between all takhi dyads. Links in the networks represented the number of agonistic or affiliative interactions occurring per hour between each takhi dyad, divided by the total number of observation hours for the study period of interest.

3.2.3.3. Developing attributes for individual takhi

3.2.3.3.1. Reproductive state

Takhi at Seer and Hustai were assigned a reproductive state based on their age, sex, and immediate reproductive history.

For the reasons discussed in Chapter 2, section 2.2.3, takhi were divided into five reproductive classes; mature stallion (male ≥ 5 years), lactating mare (female nursing a foal during the study period), non-lactating mare (female ≥ 5 years but not nursing a foal during the study period), colt (male ≤4 years), and filly (female ≤4 years and not nursing a foal during the study period). The number of individuals in each category is shown in Table 3.6. Juveniles younger than one year at the beginning of the study were not included in analysis due to the presumed dependence of their spatial and social connections on the position of their dams (Bouskila et al. 2015, Stanley et al. 2018).

Table 3.6. Count of the number of individuals in each reproductive class in the focal groups at Seer and Hustai in each season.

Location	Reproductive state		Non-breeding	Breeding
	#ID	*Name*		
Seer	1	Mature stallion	3	3
	2	Reproductive mare	13	13
	3	Non-reproductive mare	6	6
	4	Colt	8	8
	5	Filly	4	4
Hustai	1	Mature stallion	5	5
	2	Reproductive mare	17	16
	3	Non-reproductive mare	5	4
	4	Colt	7	4
	5	Filly	7	7

3.2.3.3.2. Personality type

The methods used to calculate individual personality scores for takhi at Seer, and the reason that personality scores were ultimately not obtained for Hustai takhi, have been discussed in Chapter 2.

The rated sociability scores calculated in Chapter 2 were based on the aggregated experiences of raters. The coded sociability scores were based on a narrow set of behaviours and extracted from only eight hours of observation. Although the two sociability scores were significantly positively correlated, they represented two separate units of sociability measurement, so rated and coded scores were not averaged together to create a combined sociability score. For this study the rated sociability scores were considered the most robust representation of the relative sociability of individual takhi. Therefore, the rated sociability scores, but not the coded sociability scores, were incorporated into the SNA datasets.

Takhi at Seer were assigned two personality scores; rated assertiveness, and rated sociability. Three mares could not be assigned personality scores due to a lack of repeatability in the data (see Chapter 2, section 2.3.1.2.2). Prior to incorporating the Seer personality scores into the SNA data sets, both assertiveness and sociability scores were increased by a value of three so that none of the personality scores used in the SNA would be negative.

3.2.3.3.2.1. Creating discrete personality categories

To test for a significant difference in network metrics relative to personality type, it was necessary to make personality scores discrete, rather than continuous. Using the range cut-offs listed in Table 3.7, all individuals were assigned a discrete value for each personality score as well as a continuous one, both of which were added to the attribute files for each season. Table 3.8 shows the count of individuals in each discrete personality category for each personality trait.

Table 3.7. Guidelines for the conversion of continuous personality scores to discrete personality scores for Seer takhi.

Discrete category			**Continuous score range**
	Description		
Number	*For sociability*	*For assertiveness*	
1	Very social	Very assertive	>2.0
2	Social	Assertive	>1 and <2.0
3	Mildly social	Mildly assertive	>0 and <1.0
4	Mildly antisocial	Mildly diffident	>(-1) and <0
5	Antisocial	Diffident	>(-2) and <(-1.0)
6	Very antisocial	Very diffident	<(-2.0)

Table 3.8. Count of individuals in each discrete personality category at Seer in each season, in the herd overall and within each focal group. Numbers in parentheses are the count of juveniles (colts and fillies) in each category. NB = non-breeding season and B = breeding season.

	Herd		**BRG**		**CRG**		**DIG**		**OTHER**	
Discrete personality trait	NB	B	NB	B	NB	B	NB	B	NB	B
Assertiveness										
Very assertive	2(0)	2(0)	0(0)	0(0)	2(0)	2(0)	0(0)	0(0)	0(0)	0(0)
Assertive	6(0)	6(0)	2(0)	2(0)	3(0)	3(0)	0(0)	0(0)	1(0)	1(0)
Mildly assertive	11(2)	11(2)	5(1)	4(0)	1(0)	1(0)	5(1)	4(0)	0(0)	2(2)
Mildly diffident	7(5)	7(5)	1(1)	2(2)	3(3)	1(1)	3(1)	3(1)	0(0)	1(1)
Diffident	5(5)	5(5)	2(2)	0(0)	0(0)	0(0)	3(3)	3(3)	0(0)	2(2)
Very diffident	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Sociability										
Very social	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Social	4(3)	4(3)	0(0)	0(0)	2(1)	2(1)	2(2)	1(1)	0(0)	1(1)
Mildly social	12(5)	12(5)	6(3)	3(0)	1(0)	1(0)	4(2)	4(2)	1(0)	4(3)
Mildly antisocial	10(4)	10(4)	3(1)	4(2)	6(2)	4(0)	1(1)	1(1)	0(0)	1(1)
Antisocial	2(0)	2(0)	1(0)	1(0)	0(0)	0(0)	1(0)	1(0)	0(0)	0(0)
Very antisocial	3(0)	3(0)	0(0)	0(0)	0(0)	0(0)	3(0)	3(0)	0(0)	0(0)

3.2.3.4. Summary of input data for SNA

Input data for the SNA analyses performed in Chapter 4, Chapter 5, and Chapter 6 took the form of network matrices and attribute files.

Network matrices included spatial networks and interaction networks. Spatial networks presented the median inverse distance between all takhi dyads present during the observation period of interest. Interaction networks presented interactions observed per hour across the observation period of interest. Intragroup networks only included links occurring between members of the same family group, while intergroup networks only included links occurring between members of different family groups.

Only intragroup networks were created for the Hustai data, as Hustai intergroup networks were both sparse and incomplete. Intergroup interactions were rare, and even more rarely involved the members of two of the focal groups. More often, focal group members exchanged intergroup interactions only once and with an unknown individual.

Attribute files contained information on all individuals present during the observation season. The individual information included takhi ID, reproductive state, continuous and discrete rated assertiveness and rated sociability scores, family group membership, and all observed network metrics (see section 3.2.4.1). Appendix 3.II lists the individual takhi present in the family groups at Seer (Appendix 3.II, Table 3.II.1) and Hustai (Appendix 3.II, Table 3.II.2), as well as each individual's family group membership, reproductive state, and (for Seer) personality score.

3.2.4. Applied SNA methodology

The overall aim of the SNA analyses applied in Chapter 4, Chapter 5, and Chapter 6 was to determine whether there was a significant difference in the metric scores of individuals of differing group membership, reproductive state, and personality type in the spatial and interaction networks. This was assessed through metric comparison tests.

Multiple Regression Quadratic Assignment Procedure (MRQAP) tests were also performed to determine whether individuals who were more related or more familiar (overall or when young) were more strongly connected in spatial and interaction networks. These tests were only performed in Chapter 4, and discussion of the methods applied for the analysis is continued there.

The SNA metric comparison test methods applied in Chapters 4, 5, and 6 are described below.

3.2.4.1. Calculating observed network metrics

First, the observed network metrics for all spatial and interaction networks were calculated in RStudio v. 1.0.143 (RStudio Team 2016) using the statistical package 'tnet' (Opsahl 2009). Observed network metrics (weighted betweenness, strength, weighted degree, clustering coefficient, and instrength and weighted indegree for interaction networks) were calculated and appended to the attribute file of each subpopulation using the code shown in Appendix 3.IV.

3.2.4.2. Method for testing for a significant difference in metrics relative to attribute class

All tests for a significant difference in betweenness, strength, degree, clustering coefficient (and instrength and indegree for interaction networks) among individuals of differing family group membership, reproductive state, and personality type were performed in RStudio using the statistical packages 'tnet' (Opsahl 2009), 'sna' (Butts 2016), and 'conover.test' (Dinno 2017). Weight permutations were used to explore differences in spatial network metrics, and node permutations were used to explore the differences in interaction network metrics among individuals (see section 3.2.4.2.5. for more discussion).

3.2.4.2.1. Calculating observed test statistics for metrics comparisons

For each metric permutation test, a Kruskal-Wallis one-way analysis of variance was performed on the observed network data to obtain the H test statistic of a test for a significant difference in the network metric score (for example, strength) among individuals of differing attribute class (for example, reproductive state). A Conover-Iman pairwise comparison with a Benjamini-Yekutieli p-value adjustment was performed as a post-hoc test (Dinno, pers. comm. 2017) and the observed pairwise test statistics were saved for comparison to those generated for random networks.

3.2.4.2.2. Calculating random test statistics for metrics comparisons

3.2.4.2.2.1. Digression into determining the necessary number of permutations

In the literature, the most common number of permutations, and the one used for most examples, is 1000 (Ramos-Fernandez et al. 2009, Farine 2014, Farine and Whitehead 2015). Although Whitehead (2008a) said that 1000 permutations is sufficient for most analyses, he also advised that up to 20000 permutations may be necessary if each permutation is only making very small changes to the dataset. To select a permutation count, Whitehead (2008a) recommended increasing the number of permutations by intervals with the aim of locating the point at which the p-value of the performed test of interest stabilised. For this study, Kruskal-Wallis tests were run comparing spatial network strength relative to reproductive state using 1000, 5000, 10000, and 20000 permutations of the original spatial network. Every increase in the number of permutations performed increased the precision of the p-values generated. The greatest increase in precision occurred when the number of permutations increased from 1000 to 5000. The time required to run each series of permutations increased the most when the number of permutations increased from 5000 (elapsed time = 00:02:05) to 10000 (elapsed time = 00:05:10). From consideration of both the precision of the resulting p-values and the time required to run each permutation, 5000 was selected as the number of permutations to run for all permutation tests in this study.

3.2.4.2.2.2. Calculating random test statistics

To generate the random networks serving as null models, the observed network of interest was permuted 5000 times. Following each permutation, new node metrics were calculated for the random network, and then a Kruskal-Wallis and post-hoc pairwise comparison test were performed. The random network H test statistic and pairwise tests statistics for each permutation were stored in an output file for later comparison. Then the observed network was permuted again, and the entire process was repeated.

3.2.4.2.3. Calculating p-values

Once all permutations were completed, the observed H statistic was compared to the distribution of the random H statistics. If the observed statistic was greater than 95% of the random statistics, the difference in the metric scores of individuals in different classes of the attribute of interest was considered significant. To determine where the difference occurred, the observed pairwise comparison test statistic from the post hoc test was compared to the distribution of the random pairwise comparison test statistics. If a pair (for example colts and fillies) had an observed test statistic with an absolute value greater than 95% of the absolute values of the random test statistics, they were considered to be one of the pairs to have significantly different network metrics.

3.2.4.2.4. RStudio code for metrics comparisons

The process described above was repeated for each permutation method, each metric, and each attribute of interest for each season of spatial and interaction networks at Seer and Hustai. Appendix 3.V shows an example of the RStudio code used to test for a significant difference in network metrics (betweenness, strength, degree, instrength, indegree, and clustering coefficient) relative to group membership.

3.2.4.2.5. Effectiveness of different permutation methods

During preliminary analyses, it became clear that the relative density or sparseness of the networks tested had a strong influence on the effectiveness of the different permutation methods. Interaction networks in particular were often sparse, and in the sparser networks the weight of all links in the network were often almost all the same. Charge interactions, for example, were quite rare and did not usually occur between the same individuals more than once in the same season. Thus, most of the links in the network had the same weight, and when weight permutations were performed on the network the random networks varied very little, if at all, from the observed network. When this occurred, most random test statistics were exactly the same as the observed test statistic and only a very low percentage of test statistics were either greater or less than the observed value. At other occasions, the random test statistics would be consistently lower or higher than the observed test values, but would show little to no variation beyond that. Tests where either situation occurred were considered to be undependable, as the random networks could not be considered to represent null models of the observed network structure. Two checks were used to ensure that tests with undependable results were not included in final results. To avoid test results with random test statistics that did not vary from the observed test statistic, the proportion of random test statistics either less or greater than the observed test statistic (but not the same) were summed. If the summed value was <0.9899, the test result was deemed undependable and discarded from further consideration. To avoid test results that showed no variation in the calculated random test statistic, the mean, median, and standard deviation of the 5000 random network test statistics was calculated. If the standard deviation was <0.005 the test results were discarded from further consideration.

When interaction networks were sparse, the node-level network metrics calculated were consequently sparse as well. When too few individuals in the network had metric values >0, tests for significant difference were sometimes unable to produce a test statistic, and would instead return NaN ('not a number'). All occurrences of NaN statistic results were counted and recorded in the analysis output (Appendix 3.V). If more than 50 NaN test statistics were produced, the network was considered too sparse for comparisons of that metric to produce dependable results. As an additional check, following the calculation of the observed metrics for all networks (section 3.2.4.1.) the number of takhi with metric scores >0 in the interaction network was counted. If fewer than five takhi had metric scores >0, tests for a significant difference were not performed on that metric. (See Appendix 3.VI, for checklists of the networks and metrics included or excluded from SNA for Chapter 4 [Table 3.VI.1] Chapter 5 [Table 3.VI.2], and Chapter 6 [Table 3.VI.3] depending on the sparseness of the data.

Both weight and link network permutation methods appeared to be more effective when used with the denser spatial networks. Node permutations appeared to be equally effective when used with both the spatial and interaction networks. Weight permutations were used for all significance tests involving spatial networks, and node permutations were used for all significance tests involving interaction networks. For further discussion of the effectiveness of different network permutation methods, see Chapter 7, section 7.3.1.2.

3.3. Chapter summary

This chapter provided a brief review of SNA methods, and a longer discussion of methods immediately relevant to this thesis. The process of data collection and preparation was also described. The last section of the chapter described the methodology used to obtain the results now presented in Chapter 4, Chapter 5, and Chapter 6.

4. Adult relationships: the influence of individual characteristics on the peer relationships of adult takhi in intragroup and intergroup spatial, agonistic, and affiliative networks

4.1. Introduction

According to Hinde's (1976) framework for animal societies, repeated interindividual interactions over time create relationships, and patterns of relationships in turn form a species' social structure. The relationships formed by takhi give rise to family groups and, in some populations, herds (Chapter 1, sections 1.6.4. and 1.7). Four types of relationships occur within takhi family groups: parent with offspring, mare with stallion (reproductive partners), non-reproductive peer (mares that preferentially associate, or juvenile playmates), and adult with familiar, non-offspring, juvenile. The last two relationship types can also occur outside of family groups, and may include related or familiar individuals who have dispersed and/or joined other families or bachelor groups. Intergroup relationships may contribute to the formation of herd level organisation, where multiple families maintain contact by moving together and resting together (Tong et al. 2015). Herd level organization is not seen in all takhi populations and can display varying degrees of structure and cohesion (see Chapter 1, section 1.7). The relationships that make up family groups, and potentially herds, are formed and maintained though spatial relationships, and affiliative and agonistic interactions (Hinde 1976, van Dierendonck et al. 2004, Boyd et al. 2016). This chapter will explore the influence of adult takhi peer relationships on family group and herd structure, and investigate individual characteristics which may influence the maintenance of adult relationships.

Unlike parent-offspring relationships, the relationships formed between adult takhi are the result of individual choice, and factors other than relatedness and dependency drive their formation and maintenance. Stable relationships reduce the amount of aggression encountered by all family members, which tends to increase the fitness of mares in particular (Rubenstein 1994, Linklater et al. 1999). Studies that focus on only adult relationships have found that horses tend to associate with others of the similar reproductive state, rank, and sometimes similar personality (Bouskila et al. 2015, Briard et al. 2015).

The primary categories of adult peer relationships are generally broken down in the literature by sex; mare to stallion, mare to mare, and stallion to stallion. Stable family groups in equid societies benefit family stallions by providing more exclusive access to females and greater assurance of paternity (Feh 1990, Kaseda and Khalil 1996, King et al. 2016). Stable family groups benefit mares by providing (depending on the effectiveness of the family stallion) reduced harassment from other stallions, reduced social and resource competition with non-family mares and juveniles, and overall increased opportunities for resting and grazing (Rubenstein 1994, Linklater et al. 1999).

Group fidelity in mares varies by population and by individual (Boyd et al. 2016), but long-term stable relations between a mare and stallion increase mare reproductive success (Kaseda et al. 1995, Linklater et al. 1999). Rubenstein et al. (1994) found that when reproductively active mares changed group they would join stallions lower in the interstallion hierarchy but whose rank had recently increased. A stallion with increasing rank and effectiveness can provide greater potential for long-term group stability than a stallion currently top-ranked but nearing the end of his tenure (Rubenstein 1994). The perceived success and intergroup dominance of stallions can promote long-term family cohesion and, by extension, the maintenance of mare-mare and mare-stallion bonds (Rutberg 1990, Rubenstein 1994).

Stable peer-relationships among mares have been observed to contribute to the long-term stability of family groups by reducing interindividual aggression (Berger 1977, Linklater et al. 1999). When living in a family group, mares rarely engage in affiliative interactions with peers, and peer relationships are instead characterised by maintenance of close proximity (Wells and Goldschmidt-Rothschild 1979). Mare-mare bonds can be strong enough to maintain a cohesive group in the absence of a stallion for an extended period of time (Chapter 1, section 1.6.4., Rubenstein 1994, Berger 1999), but intermare bonds may ultimately break down when former group members join a new family stallion (Rubenstein 1994).

Relationships between groups can also shape equine social structure. The formation of more or less temporary herds consisting of multiple family groups has been observed in most species of equids displaying Type I social structure (Chapter 1, section 1.7, Bouskila et al. 2015). Some studies have reported clear intergroup hierarchies that dictated each family group's access to limited resources (Berger 1977, Miller and Denniston 1979). In one population, groups that were close in rank and/or grazed together regularly would sometimes drink together without aggression (Miller and Denniston 1979). Linklater (2000) challenged whether the Miller and Denniston (1979) study observed true intergroup hierarchy, suggesting that the apparent hierarchy was merely a function of intergroup spacing and the relative dominance of stallions. The stability of family groups has not been observed to be correlated with proximity to bachelors or other family groups (Rutberg 1990), although Rubenstein and Hack (2004) proposed that in plains zebras the formation of herds reduced the risk of cuckoldry by bachelors for individual stallions.

The role of personality in shaping the form and function of group structure in free living equids has not been explored to any great extent (Bouskila et al. 2015, Briard et al. 2015). Berger (1977) incorporated an 'index of nervousness' based on individual behaviour during drinking which he tested for correlations with hesitancy to approach water sources and tendency to initiate flight. Briard et al. (2015) found significant spatial assortment by similarity in boldness in a herd of domestic mares, and found that less anxious and more explorative individuals were less gregarious.

No investigations of the relationship between individual personality and intergroup connectedness and cohesion in equid family groups were found in the literature. Studies of personality in free-living equids were either focused on the relationship between personality and intragroup cohesion (Baker 2015) or involved study populations in which the herd was consisted of multiple maternal subfamilies with no adult males present (Bouskila et al. 2015). However, research in other species has demonstrated that personality type can influence individual dominance, dispersal tendencies, and responses to stress, all of which could have an impact on social cohesion in group living species (Bremner-Harrison et al. 2004, Reale et al. 2007).

This chapter will investigate potential behavioural mechanisms promoting intra- and intergroup cohesive behaviour among adult takhi at Seer and Hustai by identifying significant trends in the relationship between the group membership, reproductive state, and personality of individuals and their importance in spatial, agonistic, and affiliative intragroup and intergroup networks. The relationship between interindividual distance and familiarity and relatedness will also be investigated. The aim of the chapter is to identify individuals with a central role in maintaining spatial and social connections between adult takhi within and between family groups.

4.2. Methods

Individuals included in the adult takhi SNA were those assigned a reproductive state of mature stallion, lactating mare, or non-lactating mare (see Appendix 3.II). Data were split by season (non-breeding or breeding), group scale (intergroup or intragroup), and, for the interaction networks, by interaction type (agonistic or affiliative).

Most of the SNA methodology applied in this chapter has been described in Chapter 3, section 3.2. Variations on that methodology are addressed in this section.

The purpose of the SNA applied in this chapter was to determine whether the centrality of individuals in adult-only networks was related to their group membership, reproductive state, or personality. Tests were performed on spatial, agonistic, and affiliative intra- and intergroup networks. A Kruskal-Wallis test followed by a Conover-Iman multiple comparisons test (described in Chapter 3, section 3.2.4.2) was used to test for a significant difference in median interindividual distances and interindividual interaction rate at both study sites. At both study locations, tests were performed separately for non-breeding and breeding seasons (see Chapter 3, section 3.2.1.1 for season definitions). Intergroup networks were not available for the Hustai data.

4.2.1. Tests for a significant relationship between interindividual distance and familiarity, youth familiarity, and relatedness

In addition to tests for a relationship between individual characteristics and network positions, tests were also performed to test for a significant correlation between interindividual distance and the familiarity, youth familiarity, and relatedness of post-dispersal adults.

4.2.1.1. Creating familiarity, youth familiarity, and relatedness data

Familiarity and relatedness matrices were created to describe the long-term relationships between the adults in focal groups.

4.2.1.1.1. Familiarity

Familiarity networks were symmetric and represented the proportion of the time that two individuals in a population occurred in the same family group. Group membership data were available for the Seer takhi from before the birth of the oldest takhi present in the populations (CA, born in 1994). Seer familiarity scores were calculated using the 'Both Identified' **association index** formula (Equation 3.8) described by Whitehead (2008a).

Equation 4.1 $x/x+y_{AB}$

Where:

x = the number of sampling periods where both A and B were observed in the same group

y_{AB} = the number of sampling periods where A and B were both observed, but were never observed in the same group.

During some years, there was only one record of group membership per month, so sampling periods were set to one-month intervals. Associations were all calculated in SocProg v. 2.6 (Whitehead 2009), and the resulting familiarity scores displayed the ratio of the number of total months each pair of individuals were observed together in the same group, divided by the total months that both individuals were observed, either together in the same group or in different groups. At Hustai, group membership data were only available from 2006 on and for six-month intervals. Thus, Hustai familiarity matrices displayed the ratio of the number of six-month sampling periods that each pair of individuals was observed together in the same group, divided by the number of six-month sampling periods during which both individuals were observed either together or in different family groups.

4.2.1.1.2. Youth familiarity

Youth familiarity networks were non-symmetric and binary, where a link value of one indicated that the takhi listed in the column was a co-group member during the first six months of life of the takhi listed in the row of the matrix. A link value of 0 indicated that the takhi listed in the column of the matrix was never a co-group member during the first six months of life of the takhi listed in the row of the matrix. At Seer, youth familiarity could be calculated for all focal individuals. At Hustai, youth familiarity could only be calculated for individuals born after 2005.

4.2.1.1.3. Relatedness

Relatedness networks (only available for Seer takhi) were symmetric. Additive relatedness was calculated for all Seer takhi (Association Takh, unpublished data) by tracing the relatedness of Seer takhi back to the founders of the captive takhi populations, using the Przewalski's horse studbook complied by Dr. Waltraut Zimmermann (Zimmermann 2012). The formula for calculating additive relatedness (Equation 3.9) was applied using the applet made available online by Christensen (2017).

Equation 4.4 $$a_{XY} = (a_{XA} + a_{XB})/2$$

Where:
X = the older of the two animals for whom relatedness is being calculated
Y = the younger of the two animals for whom relatedness is being calculated
A and B = the parents of Y
a_{XY} = the additive relatedness of X and Y
a_{XA} = the additive relatedness of X and A
a_{XB} = the additive relatedness of X and B

Relatedness data were not available for the Hustai focal takhi.

4.2.1.2. Testing for correlations between spatial and relationship networks using Multiple Regression Quadratic Assignment Procedure

The Multiple Regression Quadratic Assignment Procedure (MRQAP) was used to test for significant correlations between spatial matrices and the familiarity, youth familiarity, and relatedness matrices of takhi at both sites. The MRQAP is a method for exploring the relationship between matrices X (the dependent matrix) and Y (an independent predictor) while controlling for the effect of several matrices Z (also independent) (Dekker et al. 2007, Whitehead 2015). The MRQAP is an extension of the bivariate Mantel's Z test (Mantel 1967) which tests for a significant relationship between two matrices that include the same individuals (Whitehead 2008a). MRQAP tests performed in SocProg v. 2.6 (Whitehead 2009) used Dekker et al. (2007)'s double semi-partialing method, which calculates the p value by randomizing the residuals from the regression on each predictor variable (Bouskila et al. 2015).

MRQAP tests were used to test the relationship between each dyad's median interindividual distance and their familiarity, youth familiarity, and relatedness, while controlling for the effect of the other matrices and for similarity of reproductive state. All MRQAP tests were performed in SocProg v. 2.6 (Whitehead 2009). Previously created spatial, interaction, familiarity, youth familiarity, and relatedness matrices and attribute files were imported into SocProg for analysis. All MRQAP tests were performed with 5000 permutations.

4.2.2. Review of network metrics interpretation

In the results presented below, sections 4.3.1, 4.3.2, and 4.3.3 present the results of tests for a significant difference in centrality among individuals using several network metrics. The summary table from Chapter 3, section 3.1.2.4 defining and interpreting each network metric is reproduced here for ease of reference within the chapter (Table 4.1). Further definitions of SNA terminology can be found in the glossary in Chapter 3, Appendix 3.I.

Table 4.1. A summary of how the network metrics applied in this study are interpreted in the context of spatial and interaction networks.

Network metric	**Measures…**	**Individuals with a high score…**
Strength	…the strength of connections (or of given connections, for directed networks).	…are very close to, or give many interactions to, a few or many individuals.
Degree	…the number *and* strength of connections (or of given connections, for directed networks).	…are very close to, or give many interactions to, many individuals, but will have an even higher score if the connections are strong.
Instrength	…the strength of received connection.	…receive many interactions.
Indegree	…the number *and* strength of received connections.	…receive interactions from many individuals, but will have an even higher score if they receive many interactions.
Betweenness	…the individual's importance as a connection broker.	…are the bridge connecting many individuals either spatially or through interactions.
Clustering coefficient	…the number and strength of well connected neighbours.	…are close to many neighbours that are also close to each other, or interact with individuals who also interact with each other.

4.3. Results

Individuals included in the adult takhi SNA included a total of 22 individuals at Seer (3 stallions, 13 lactating mares, and 6 non-lactating mares) and 27 individuals at Hustai (5 stallions, 16 to 17 lactating mares, and 4 to 5 non-lactating mares).

A count of the intragroup and intergroup agonistic and affiliative interactions occurring between adult takhi is shown in Table 4.2.

Table 4.2. Count of interaction occurrences at Seer and Hustai involving only adult takhi, broken down by type, season, and intragroup and intergroup occurrence.

Location		Interaction	Non-breeding		Breeding		Total		
			Intra	Inter	Intra	Inter	Intra	Inter	Overall
Seer	Agonistic	**Total**	**105**	**73**	**73**	**31**	**178**	**104**	**282**
		Charge	10	15	4	9	14	24	**38**
		Chase	0	0	0	5	0	5	**5**
		Head threat	95	58	69	17	164	75	**239**
	Affiliative	**Total**	**10**	**0**	**10**	**0**	**20**	**0**	**20**
		Mutual grooming	8	0	10	0	18	0	**18**
		Play	2	0	0	0	2	0	**2**
Hustai	Agonistic	**Total**	**24**		**79**		**103**	**0**	**103**
		Charge	4		8		12	0	**12**
		Chase	0		2		2	0	**2**
		Head threat	20		69		89	0	**89**
	Affiliative	**Total**	**6**		**32**		**38**	**0**	**38**
		Mutual grooming	6		28		34	0	**34**
		Play	0		4		0	0	**4**

4.3.1. Significant differences in adult centrality relative to group membership

The results of tests for a significant difference in network metrics relative to group membership are presented in Table 4.3.

At Seer, significant differences were seen in the intergroup spatial networks and intragroup agonistic networks in both non-breeding and breeding seasons, although not consistently across all metrics. CRG had greater betweenness, strength, and degree than all other groups in both seasons (although not degree in the breeding season). During the non-breeding season BRG had greater strength than DIG. DIG and OTHER tended to have the highest cluster scores. CRG was very central to the intergroup spatial network overall.

Table 4.3. Significant pairwise differences in spatial, agonistic, and affiliative network metrics among adults relative to group membership at Seer and Hustai. *ns* indicated no significant differences were detected in that network. *NA* indicates no tests were performed for that study site.

Location	Scale	Network	Metric	Season	Group(s)…		…group(s)
Seer	Inter	Spatial	Betweenness	NB/B	CRG...	…had significantly greater metric values than…	...BRG, DIG, OTHER
			Strength	NB	CRG…		...BRG, DIG, OTHER
				NB	BRG…		...DIG, OTHER
				B	CRG…		...BRG, DIG, OTHER
			Degree	NB	CRG…		...BRG, DIG, OTHER
				NB	BRG…		...OTHER
			Cluster	NB	DIG, OTHER…		...BRG
				B	BRG…		...CRG
				B	DIG…		...BRG, CRG
				B	OTHER…		...BRG, CRG, DIG
		Agonistic	*ns*				
		Affiliative	*ns*				
	Intra	Spatial	*ns*				
		Agonistic	Strength/ Degree	B	CRG…		...BRG, DIG, OTHER
			Cluster	NB	BRG, CRG…		...DIG, OTHER
				B	CRG…		...BRG, OTHER
		Affiliative	*ns*				
Hustai	Inter	*NA*					
	Intra	Spatial	Betweenness	NB	DNG, ZRG…		...BDG, KEG
		Agonistic	Betweenness	NB	ZRG…		...BDG, DNG, KEG, WNG
			Cluster	NB	KEG…		...BDG, DNG, WNG
				NB	ZRG…		...BDG, DNG, KEG, WNG
				B	BDG, DNG, ZRG…		...WNG
				B	ZRG…		...KEG
		Affiliative	*ns*				

Location: Field site.

Scale: If 'Inter' the network only deals with intergroup links, if 'Intra' the network only deals with intragroup links.

Network: The spatial or interaction network for which metrics were calculated.

Metric: Network metric for which significant difference is being tested (see definitions overview in section 4.2.2).

Season: Study period (see section 3.2.1.1 for exact dates). NB = non-breeding season and B = breeding season.

Members of CRG tended to be much closer to the members of other groups than were members of BRG, DIG, or OTHER. The high cluster scores of the other groups occurred because they were all connected to the strongly interconnected members of CRG.

During the breeding season CRG had higher agonistic strength and degree and higher cluster scores than some of the other groups during both seasons. Within their group, members of CRG were significantly more likely to initiate agonistic interactions during the breeding season, but the trend was not strong, as members were not also more likely to receive agonistic interactions.

In the non-breeding season one individual each in DNG and ZRG had a very high betweenness score for the spatial network, which resulted in the two groups overall having significantly greater betweenness than BDG and KEG. ZRG was the only group fully connected by agonistic interactions and had significantly greater betweenness than the other groups. Significant trends in cluster score in non-breeding and breeding networks only served to differentiate groups where no interactions occurred from groups were some interactions occurred.

4.3.2. Significant differences in adult centrality relative to reproductive state

The results of tests for a significant difference in network metrics relative to reproductive state are presented in Table 4.4.

At Seer, significant differences were seen in the intergroup agonistic and intragroup spatial networks. Stallions had significantly higher agonistic intergroup strength and degree scores than mares in both the breeding and non-breeding season. In the non-breeding season stallions also had significantly greater betweenness than mares.

The high spatial intragroup betweenness, strength, and degree of non-lactating mares is due to the high centrality of one mare, AR, who changed groups during the non-breeding season and thus had intragroup connections to two family groups.

At Hustai, there were significant differences in the intragroup spatial and agonistic networks. The high strength and degree of lactating mares in the non-breeding spatial network was primarily because there were only non-lactating mares in two groups, and stallions were not spatially central. Non-lactating mares had high betweenness, instrength, and indegree in the non-breeding agonistic network because of a high rate of interaction among ZRG group members, all but one of whom were non-lactating.

Table 4.4. Significant pairwise differences in spatial, agonistic, and affiliative network metrics among adults relative to reproductive state at Seer and Hustai. *ns* indicated no significant differences were detected in that network. *NA* indicates no tests were performed for that study site.

Location	Scale	Network	Metric	Season	Reproductive class(es)…	…had significantly greater metric values than…	…reproductive class(es)
Seer	Inter	Spatial	*ns*				
		Agonistic	Betweenness	NB	Stallions…		...all mares
			Strength/Degree	NB/B	Stallions…		...all mares
		Affiliative	*ns*				
	Intra	Spatial	Betweenness	NB	Non-lactating mares…		...lactating mares
			Strength/Degree	NB	Non-lactating mares…		...lactating mares, stallions
		Agonistic	*ns*				
		Affiliative	*ns*				
Hustai	Inter	*NA*					
	Intra	Spatial	Strength/Degree	NB	Lactating mares…		...stallions
		Agonistic	Betweenness	NB	Non-lactating mares…		...lactating mares, stallions
			Instrength/Indegree	NB	Non-lactating mares…		...lactating mares, stallions
		Affiliative	*ns*				

Location: Field site.

Scale: If 'Inter' the network only deals with intergroup links, if 'Intra' the network only deals with intragroup links.

Network: The spatial or interaction network for which metrics were calculated.
Metric: Network metric for which significant difference is being tested (see definitions overview in section 4.2.2).

Season: Study period (see section 3.2.1.1 for exact dates). NB = non-breeding season and B = breeding season.

4.3.3. Significant differences in adult centrality relative to personality (Seer only)

Significant differences relative to personality were seen in the intergroup spatial and agonistic networks and the intragroup spatial, agonistic, and affiliative networks at Seer (Table 4.5).

Mildly antisocial and social takhi tended to be more central in the intergroup spatial networks. This trend was related to the centrality of CRG, as four of the six mildly antisocial adults were members of CRG. However, the mildly antisocial members of BRG also had high betweenness, and higher strength and degree scores than mildly social and very antisocial individuals. Cluster score trends relative to assertiveness during the breeding season were also related to group membership.

Assertive takhi, all mares, received significantly more intergroup agonistic interactions than mildly assertive and mildly diffident takhi during the non-breeding season.

Social and mildly antisocial individuals had significantly higher strength than mildly social and antisocial takhi in intragroup spatial networks in the non-breeding and breeding seasons. These trends appeared to be the result of the general cohesiveness of CRG, the central position of the one mildly antisocial mare in BRG, and (during the non-breeding season) the bridging position of AR. Very antisocial takhi also had high strength, because of the tendency of the Prague mares (CI, LI, and KD) to stay close to each other and to AR. Mildly antisocial takhi also received significantly more agonistic interactions than other takhi during the non-breeding season. The significantly high giving and receiving of affiliative interactions by antisocial takhi was because AH was frequently involved in mutual grooming in the otherwise very sparse affiliative intragroup interaction network.

Table 4.5. Significant pairwise differences in spatial, agonistic, and affiliative network metrics among adults relative to personality at Seer. *ns* indicated no significant differences were detected in that network.

Scale	Network	Metric	Attribute	Season	Personality class(es)…		…personality class(es)
Inter	Spatial	Betweenness	Sociable	NB	Social, mildly antisocial…	**…had significantly greater metric values than…**	...mildly social, antisocial, very antisocial
		Strength/Degree	Sociable	NB	Social, mildly antisocial…		...mildly social, antisocial, very antisocial
				B	Social, mildly antisocial…		...mildly social
		Cluster	Assertive	B	Mildly assertive, mildly diffident…		...very assertive
	Agonistic	Instrength/Indegree	Assertive	NB	Assertive…		...mildly assertive, mildly diffident
	Affiliative	*ns*					
Intra	Spatial	Strength	Sociable	NB	Social, mildly antisocial…		...mildly social
				NB	Very antisocial…		...mildly social, antisocial
				B	Social…		...mildly social, antisocial
				B	Mildly antisocial…		...mildly social
	Agonistic	Instrength	Sociable	NB	Mildly antisocial…		...mildly social, antisocial
	Affiliative	Strength/Degree	Sociable	B	Antisocial…		...social, mildly social, mildly antisocial, very antisocial
		Instrength/Indegree	Sociable	B	Antisocial…		...social, mildly social, mildly antisocial, very antisocial

Scale: If 'Inter' the network only deals with intergroup links, if 'Intra' the network only deals with intragroup links.

Network: The spatial or interaction network for which metrics were calculated.

Metric: Network metric for which significant difference is being tested (see definitions overview in section 4.2.2).

Attribute: Personality trait for which a significant difference in metrics is being tested.

Season: Study period (see section 3.2.1.1 for exact dates). NB = non-breeding season and B = breeding season.

4.3.4. Relationships between interindividual distance and relatedness and familiarity

MRQAP tests for a relationship between interindividual distance and takhi familiarity, youth familiarity, and relatedness, while also controlling for similarity of reproductive state, found a positive correlation between interindividual distance and familiarity at both locations and across both seasons (Table 4.6).

Table 4.6. Results of MRQAP tests for a significant relationship between interindividual distance and familiarity, youth familiarity, and relatedness (Seer only) at Seer and Hustai.

Location	Season	Network	Partial correlation coefficient	P-value
Seer	Non-breeding	Familiarity	0.551	**0.0000**
		Youth Familiarity	-0.167	**0.0004**
		Relatedness	0.058	0.4756
		Reproductive state	-0.032	0.7944
	Breeding	Familiarity	0.574	**0.0000**
		Youth Familiarity	-0.164	**0.0000**
		Relatedness	0.049	0.5020
		Reproductive state	-0.006	0.9828
Hustai	Non-breeding	Familiarity	0.552	**0.0000**
		Youth Familiarity	-0.048	0.2264
		Reproductive state	0.149	**0.0172**
	Breeding	Familiarity	0.736	**0.0000**
		Youth Familiarity	-0.075	0.1788
		Reproductive state	0.079	0.2868

At Seer there was also a significant negative correlation between interindividual distance and youth familiarity. At Hustai there was a positive correlation between interindividual distance and reproductive state in the non-breeding season.

4.3.5. Summary of results

The strongest and most consistent results observed in these analyses were the centrality of CRG intergroup spatial networks, and the position of stallions as the bridge and primary originators of intergroup agonistic interactions.

Significant intragroup spatial trends were only observed during the non-breeding season at Seer and Hustai. At Hustai, lactating mares tended to be more central, primarily because there were few non-lactating mares and stallions were spatially peripheral. At Seer, non-lactating mares were more central, although that was primarily due to AR’s connection to two family groups.

Interindividual distance was significantly positively correlated with familiarity at Seer and Hustai. At Seer there was also a negative correlation between interindividual distance and youth familiarity.

At Seer, social and mildly antisocial takhi tended to be the most strongly connected in inter- and intragroup networks in non-breeding and breeding seasons. This trend may be related to the personality make-up of CRG, which contained the only social adult and many mildly antisocial individuals. However, mildly antisocial individuals in BRG also had high metric scores.

Affiliative networks were very sparse. Affiliative interactions between adult peers intragroup were very rare, and they never occurred between members of different groups.

4.4. Discussion

Individual centrality in adult takhi networks was related to group membership, personality, and reproductive state. Members of CRG were significantly more likely to be close to non-group members than were individuals from other groups. Trends in personality were related to the personality make-up of CRG, but social and mildly social individuals were more strongly connected to the members of other groups in spatial networks. Stallions gave the most intergroup agonistic interactions and assertive individuals received more intergroup agonistic interactions.

4.4.1. The high centrality of CRG in intergroup networks

Adults in CRG tended to be significantly closer to non-group members than were the members of other groups (Figure 4.1a, c). The centrality of CRG was largely a reflection of the fact that CRG was the group least likely to travel alone. During both the non-breeding and breeding season, BRG and DIG, but never CRG, would occasionally rest and travel separately from the other groups for a few hours up to a few days. As a result, the median distance between CRG takhi and the members of other groups over each observation season was lower than the median distance between BRG and DIG members. Three possible reasons for the greater cohesive tendencies of CRG are group seniority, group personality makeup, and the influence of highly active members.

The mean and median age of CRG adults ($\bar{x}$=11.67, $\tilde{x}$=12.29) was greater than BRG ($\bar{x}$=8.89, $\tilde{x}$=6.08) and DIG ($\bar{x}$=10.4, $\tilde{x}$=9.75) and CR is a year older than BR and DI. Of the five mares in CRG, three (AS, CL, and DB) have been co-group members since before CR joined them as the family stallion in 2007, and (with some occasional shuffling) they and CR have been an established family group since he joined them. The seniority of the group overall, their long-term stability, and the seniority of the stallion may mean that CRG, and CR particularly, are less apt to feel threatened by the proximity of other groups. Rutberg (1990) found that older stallions had more stable groups, although they were also more apt to lose mares than to gain them. It is possible that as CR ages and more colts mature enough to challenge him, both the stability and the centrality of CRG will decrease.

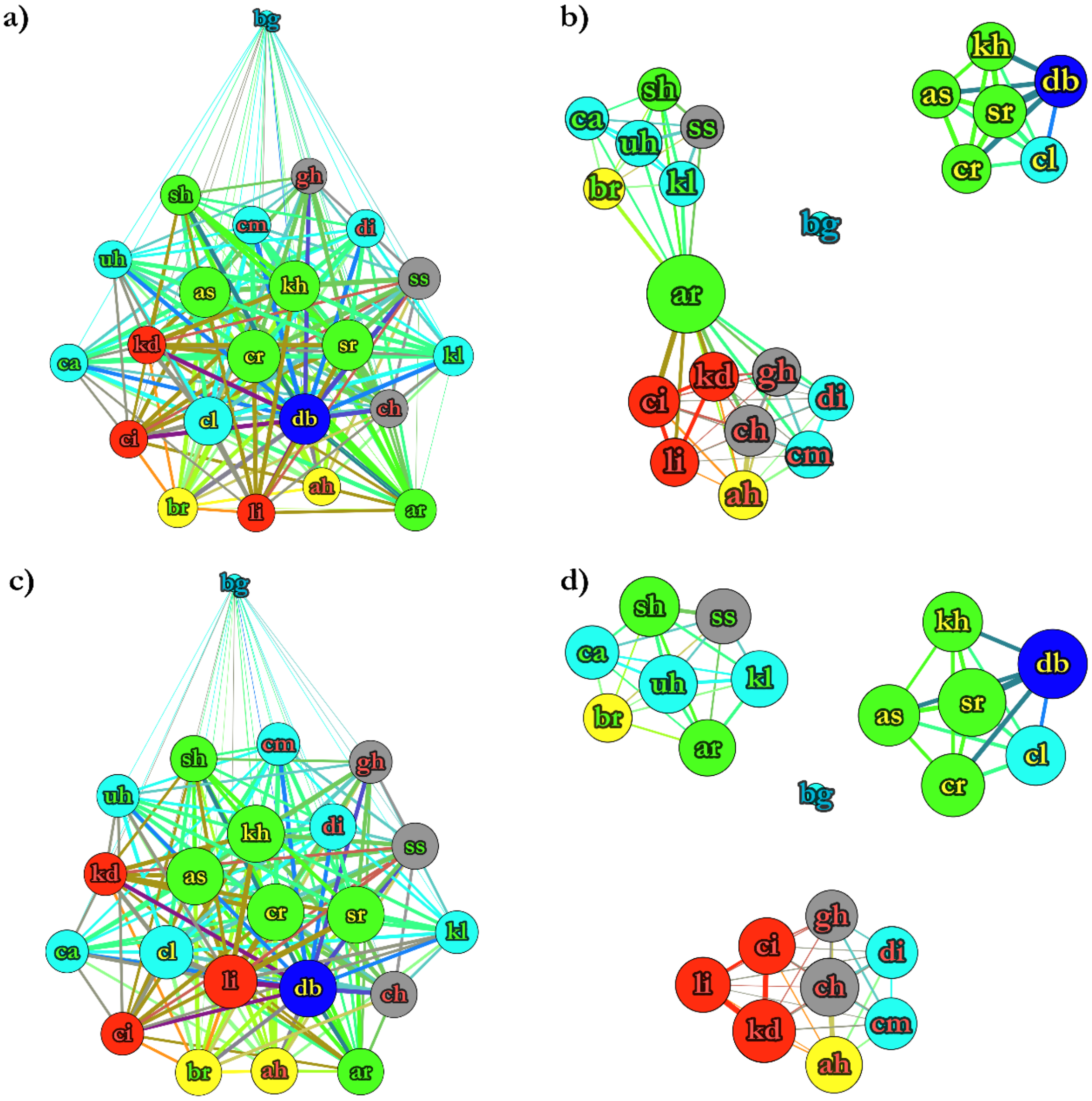


Figure 4.1. Sociograms of the Seer non-breeding (a) intergroup and (b) intragroup and breeding (c) intergroup and (d) intragroup spatial networks. Node size represents network strength score. Node colour indicates discrete sociability score; blue = social, sky blue = mildly social, green = mildly antisocial, yellow = antisocial, red = very antisocial, and grey = no personality score assigned. Label colour indicates group membership; green = BRG, yellow = CRG, red = DIG, and blue = OTHER.

The significant difference in intergroup spatial network score relative to personality appeared to be related to the intergroup centrality of CRG. Only one adult takhi, DB, a non-lactating mare in CRG, was classed as social. Of the six mildly antisocial adults, four were members of CRG (Figure 4.1). The most parsimonious explanation is that trends in personality are due to the centrality of CRG members, not vice versa. Significant differences in metric score relative to group membership were more consistent across multiple seasons than were personality trends. However, Baker (2015) found trends in personality relative to group membership in some, but not all, of her focal family groups. Further research should explore the relationship between the personality make-up of groups and their inter- and intragroup cohesiveness.

CR was more frequently observed to engage in affiliative intergroup interactions than the other family stallions. DB was the only adult mare observed to engage in affiliative intergroup interactions, and occupied a non-significant but still spatially central position in both breeding and non-breeding intragroup networks (Figure 4.1). Both CR and DB also had the highest assertiveness scores of the Seer population (Chapter 2, Figure 2.3b). Thus, it may be that high social activity of these two individuals in CRG contributed to the observed centrality of CRG as a group.

The high centrality of CRG adults as a group suggests that, spatially, CRG members could have the opportunity to act as brokers or liaisons between BRG and DIG. Miller and Denniston (1979) noted that groups of similar dominance rank could graze together in close proximity without visible aggression between group members. Rutberg (1990) observed that some family groups had a greater tolerance of close proximity to other family groups and bachelors. Neither study mentioned potential causes of increased tolerance beyond similar rank. From this study it appears that group personality trends and the presence of key individuals may play a role. Further research should track the influence of CRG on herd cohesion, particularly as CR begins to face more challenges from young stallions.

4.4.2. Role of familiarity

The positive correlation between familiarity and interindividual distance is closely tied to group membership. Members of the same group tended to be closer to each other than to the members of other groups (part of the definition of a group) and familiarity was defined by co-group membership across takhi lifetimes (see section 4.2.1.1.1). However, the results underscore the stability of the family groups at both locations. Familiarity calculations were based on co-group membership relative to co-occurrence for all horse from 1998 to 2015 at Seer, and from 2006 to 2015 at Hustai. The fact that familiarity scores based on up to 26 years of association are significantly correlated with present day interindividual distance measures emphasises the long-term stability of the takhi social groups.

The negative correlation between youth familiarity and interindividual distance supports current understanding of youth familiarity as a mechanism for inbreeding avoidance, where juveniles of both sexes avoid breeding with members of their natal group (Duncan et al. 1984, Berger and Cunningham 1987, Monard et al. 1996). Youth familiarity data for Hustai was incomplete, as information was only available for takhi born after 2005, so the lack of significant trends was not surprising.

The positive correlation between interindividual distance and reproductive state observed at Hustai in the non-breeding season probably occurred because almost all non-lactating mares were in one group, ZRG, and in all groups stallions tended to be peripheral in spatial networks. As a result, lactating mares were closer to each other than to their stallions, and the non-lactating mares from ZRG were also clustered together.

There was no correlation between interindividual distance and relatedness at Seer. Tong et al. (2015) found that plains zebra herds made up of multiple family groups had significantly higher relatedness among females in the associating groups than would be expected by chance. The small size of the population at Seer and relatively high relatedness of all individuals would make any relationship between relatedness and interindividual distance challenging to detect.

4.4.3. Affiliative networks

Affiliative interactions between adults were rare, particularly at Seer. Play occurred on only one occasion at both Seer and Hustai (Table 4.2). Mutual grooming occurred more frequently (Table 4.2). At Hustai, agonistic and affiliative interactions occurred in roughly equal proportion in both seasons (Table 4.2). At Seer agonistic interactions occurred much more frequently than affiliative ones.

Previous studies have found that juveniles participate more frequently in mutual grooming than adults (Wells and Goldschmidt-Rothschild 1979, Boyd 1988a), although others have found that mares initiated more mutual grooming than juveniles (Keiper and Receveur 1992). Sigurjonsdottir et al. (2003) found that adult mares tended to mutual groom more with peers and at higher rates when no stallion was present, while in populations with a mature stallion, mutual grooming was more often observed within maternal subfamilies than between peers (Feist and McCullough 1976, Wells and Goldschmidt-Rothschild 1979). In groups with stallions, intermare affiliative relationships are often reflected more by proximity maintenance than by active interaction (Wells and Goldschmidt-Rothschild 1979). It may be that when Type I equids form larger, more loosely structured groups where multiple social partners are available and stallions aren’t actively maintaining family group borders, it is beneficial for mares to actively and pre-emptively manage established social bonds through affiliative interactions.

The high ratio of agonistic to affiliative interaction between peers at Seer may be because the groups are stable enough that affiliative interactions as a peace-keeping measure are not necessary. The even distribution of agonistic and affiliative interactions at Hustai may just be due to the small size of the dataset. King's (2002) study of the Hustai population found that affiliative interactions were much less common than agonistic ones, and occurred more often between mares and juveniles than between adult peers. Further research is necessary to determine whether the even ratio of agonistic to affiliative interactions at Hustai has any other cause beyond sparsity of data. The limitations of the Hustai data set will be discussed in more detail in Chapter 7, section 7.3.4.

4.4.4. Centrality of stallions in intergroup agonistic networks

Stallions at Seer gave significantly more and more frequent intergroup agonistic interactions than mares. If mares join stallions in part to minimise the need for engagement in intergroup agonistic interaction (Rubenstein 1994), the greater intergroup centrality of family stallions relative to mares is a logical result. This trend was stronger in the non-breeding season (Figure 4.2a) (where stallions also had significantly greater betweenness than mares) than in the breeding season (Figure 4.2d). Weaker trends in the breeding season occurred because fewer intergroup interactions occurred during the breeding season overall, and lactating mares were more active due to the presence of young foals (Figure 4.2d, e).

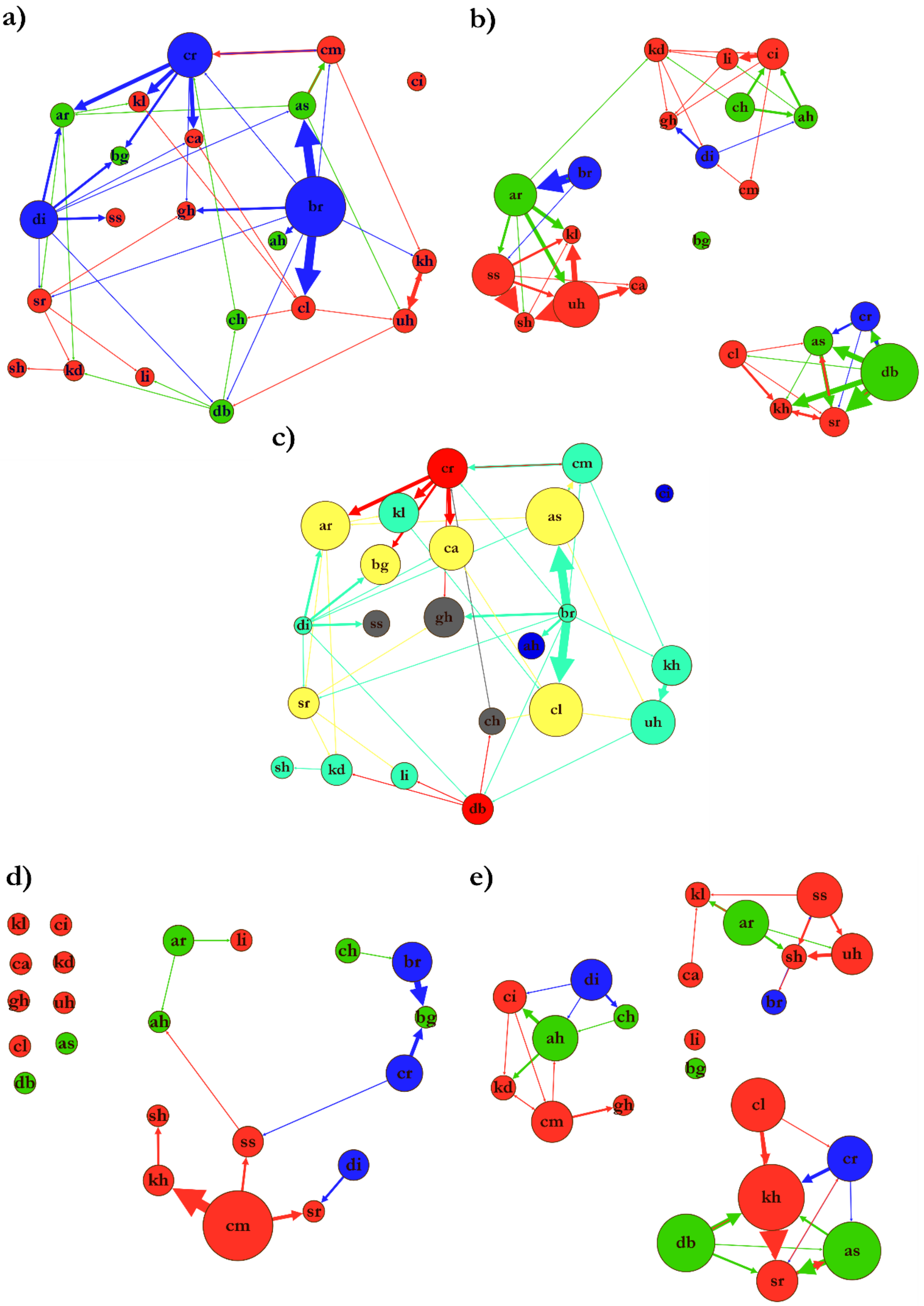


Figure 4.2. Sociogram showing Seer non-breeding (a; c) intergroup and (b) intragroup and breeding (d) intergroup and (e) intragroup agonistic networks. For sociograms a, b, d, and e, node size represents network strength and colour represents reproductive state; red = lactating mare, green = non-lactating mare, and blue = stallion. For sociogram c, node size represents network instrength and node colour represents assertiveness; red = very assertive, yellow = assertive, teal = mildly assertive, blue = mildly diffident, and grey = no score assessed.

Overall, stallions at Seer appear to be the most active managers of intergroup cohesion. Similar trends were observed at Hustai, although the networks were too incomplete for analysis (Davie, unpublished data). Similar conclusions have also been reached by other studies. Rubenstein (1994) found that the intermale dominance of the family stallion often dictated the freedom of movement allowed to the family group. Duncan and Vigne (1979) found small groups kept away from larger groups because of stallion intolerance, while Rubenstein and Hack (2004) proposed that plains zebra herds formed in part to reduce the pressure of bachelors on individual family stallions. Ozogány and Vicsek's (2015) herd structure model, which successfully recreated the herd structure observed in the Hortobágy Nature Reserve takhi population, was based on the creation of family groups with one 'leader' individual. Although no evidence has been found of one leader in actual Type I equid populations (Krueger et al. 2014, Bourjade et al. 2015), the results of the model suggest the presence one or more individuals managing family group borders may have an important role in the formation or lack of formation of larger herds.

Only one interaction link occurred between stallions in the agonistic networks (Figure 4.2a). Although the three stallions were frequently observed to interact, they did not exchange any of the focal interactions included in the agonistic networks. Rather, the three interactions most frequently exchanged were strike (n=49; 42% of all interstallion interactions), kick (n=26; 22%), and kick threat (n=10; 9%) (see Appendix 3.III for interaction definitions). Stallions thus did not exchange intergroup interactions with a spatial management component with each other. Instead the interactions were directed at the mares of other groups.

Previous studies have reported most intergroup interactions occurring between family stallions or between stallions and bachelors (Feist and McCullough 1976, Berger 1977, Duncan and Vigne 1979, Rubenstein 1981, Rutberg 1990). Mares were also observed to be involved in intergroup interactions, but usually less frequently (Feist and McCullough 1976, Berger 1977, Rutberg 1990). Feist and McCullough (1976) reported strike and charge interactions as used exclusively by stallions, which was not the case at Seer or Hustai. However, Feist and McCullough (1976) also observed that stallions generally used strikes when interacting with each other and used charge interactions when interacting with the members of other groups. Feral stallions in the US Grand Canyon began 80% of interstallion encounters with a strike interaction (Berger 1977). Both Feist and McCullough (1976) and Rubenstein (1981) observed that stallions will chase each other in escalated encounters, particularly at the end of confrontations. Chase interactions are one of the spatial management interactions included in the agonistic networks. However, no serious fights occurred between stallions at Seer during the study period. Although stallions were also active in intragroup agonistic networks in both the non-breeding (Figure 4.2b) and breeding (Figure 4.2e) season, they were not more active than mares.

Assertive takhi, all of whom were mares, had significantly greater agonistic interaction instrength in the non-breeding season (Figure 4.2c). The assertive mares received most of the interactions directed by stallions toward other groups. The same trend was not observed in the breeding season, but this may have been because the network was too sparse. Further research should explore why assertive mares would receive more intergroup agonistic interactions. It may be that they are most likely to push group boundaries, or stallions may be targeting them for other reasons.

4.5. Chapter Outcomes

The purpose of this chapter was to assess whether the group membership, reproductive state, or personality of adult takhi influenced their centrality in intragroup and intergroup spatial, agonistic, and affiliative networks.

Main chapter findings were as follows:

- The group CRG was significantly more central to the Seer intergroup spatial network in non-breeding and breeding seasons. Members of CRG were significantly more likely to be close to the members of other groups than were members of BRG, DIG, or OTHER. It is unclear whether this tendency is related to the seniority and long-term stability of CRG, the personality profile of the group, or the presence of very socially active individuals in the group, particularly DB and CR.
- More familiar individuals tended to be closer together. Individuals tended to be farther away from conspecifics who had been present in their natal group.
- Stallions were significantly more central in intergroup interaction networks than mares. They offered more intergroup agonistic interactions, and mares from other groups, not stallions, were the recipients. In the non-breeding season assertive mares received significantly more agonistic interactions than did very assertive mares and more diffident individuals.

The following chapters will investigate whether group membership, reproductive state, and personality had a significant influence on peer relationships among juveniles (Chapter 5) and cross-age relationships between adults and juveniles (Chapter 6) in intragroup and intergroup spatial, agonistic, and affiliative networks.

5. Juveniles relationships: the influence of individual characteristics on the peer relationships of juvenile takhi in intragroup and intergroup spatial, agonistic, and affiliative networks

5.1. Introduction

The adult peer relationships discussed in Chapter 4 first began to be formed when the now adults were pre-dispersal juveniles, with many of them living in the same group, in neighbouring groups in the same herd, or joining the same post-dispersal bachelor or mixed-sex groups. The peer relationships of juveniles in the current takhi family groups will influence their relationships as adults, and as a result will shape the future group and herd social structures of the Seer and Hustai populations.

Familiarity and inbreeding avoidance dictate which individuals may join to form family groups, and thus juvenile relationships influence the formation and quality of adult inter- and intragroup relationships. Feral horses and takhi use familiarity as a mechanism for inbreeding avoidance and can recognise parents, offspring, and peers (Duncan et al. 1984, Berger and Cunningham 1987, Monard et al. 1996). When fillies disperse they avoid joining colts or young stallions who were members of their natal group (Monard et al. 1996), but will often move to a group containing familiar females (Monard et al. 1996, Bouskila et al. 2015). Tong et al. (2015) found that plains zebra herds made up of multiple family groups had significantly higher relatedness among females in the associating groups than would be expected by chance. Stallions have been observed to responded aggressively to unfamiliar bachelors but to play with those who were familiar (Berger and Cunningham 1987). Thus, the relationships formed between juvenile peers can contribute to the social structure of the same individuals as adults.

The characteristics of peer relationships in juvenile equids have been observed by many studies to differ between the sexes. Multiple studies have found colts play more than fillies (Boyd 1988a, Sigurjónsdóttir et al. 2003, King et al. 2016) although others have found differences in play quality but not play rate between the sexes (Cameron et al. 2008). Juveniles play to develop motor and social skills (Khalil and Kaseda 1998, Cameron et al. 2008, King et al. 2016). Play is of particular importance for colts, whose reproductive success as adults depends on their effectiveness when engaging in both agonistic and affiliative interactions (Berger 1986, Khalil and Kaseda 1998). Camargue colts, but not fillies, appeared to actively seek to build relationships with stallions and colts in other groups (Wells and Goldschmidt-Rothschild 1979).

Crowell-Davis et al. (1986) found that fillies groomed more with peers of both sexes, and proposed that the high rate of grooming was practise for forming stronger female-female bonds later in life. Thus, sex has been observed to have an influence on the type and quality of the relationships formed between juveniles.

Personality and group membership have been mentioned by previous studies as having a potential influence on juvenile peer relationships, but were generally not the focus of the studies in which they were included. Sigurjondottir et al. (2003) observed that some juveniles were more popular as playmates in a herd of Icelandic horses, and suggested that popularity may have been related to personality type, but did not assess personality as part of the study. Nuñez et al. (2015) used network centrality, specifically degree and strength, to assess juvenile sociability. They found that more social individuals, specifically those with higher network degree, were more likely to survive a catastrophic event. Stanley and Shultz (2012) found family group membership to be a significant factor influencing the closeness and betweenness scores of juveniles in social networks including relationships between individuals of all ages and reproductive states, but did not offer an explanation for the observed trend.

Sex, personality, and group membership are all factors with a potential influence on the type and strength of juvenile peer relationships. This chapter will explore how current juvenile non-reproductive peer relationships at Seer and Hustai connect individuals within and between family groups. This will be done by testing the influence of individual group membership, sex, and personality on the centrality of individuals in juvenile intragroup and intergroup spatial, affiliative, and agonistic networks.

5.2. Methods

Individuals included in the juvenile takhi SNA were those assigned a reproductive state of colt or filly (see Appendix 3.II, Table 3.II.1), and included all juveniles who were over one year old at the beginning of the study. Because there were only two reproductive states in the juvenile category, a Wilcoxon-Mann-Whitney U test was used instead of a Kruskal-Wallis test to compare centrality by reproductive state (essentially by sex) (see Appendix 5.I for an example of RStudio code for testing differences in juvenile network centrality by sex). As juveniles are not reproductively active, networks were not split by non-breeding/breeding season. Tests for group membership were based on natal group membership, although some juveniles had dispersed by the end of the study. Natal group membership was considered to have a greater probable influence on the peer relationships of juveniles, as dispersing juveniles had been in their natal group for two to four years, none had dispersed at the beginning of the study, and they were in their post-dispersal group for a maximum of six months by the end of the study.

Further, the focus of this chapter was on juvenile relationships pre-dispersal. See Appendix 3.II, Table 3.II.1 for the group membership of juveniles in the non-breeding season (used for analysis) and breeding season. Spatial, agonistic, and affiliative networks and all attribute data were assembled using the methods described in Chapter 3, section 3.2.3. Tests for a relationship between spatial distribution and familiarity, youth familiarity, and relatedness were not performed. Familiarity and youth familiarity scores were based on group membership over time. All juveniles were pre-dispersal at the beginning of the study, so group membership, familiarity, and youth familiarity were essentially the same measure.

5.2.1. Review of network metrics interpretation

Presented below are the results of tests for a significant difference in centrality among individuals using several network metrics. The summary table from Chapter 3, section 3.1.2.4 (Table 3.1) describing the importance of each network metric type is reproduced below for ease of reference within the chapter (Table 5.1). Further definitions of network terminology can be found in the glossary in Chapter 3, Appendix 3.I.

Table 5.1. A summary of how the network metrics applied in this study are interpreted in the context of spatial and interaction networks.

Network metric	Measures…	Individuals with a high score…
Strength	…the strength of connections (or of given connections, for directed networks).	…are very close to, or give many interactions to, a few or many individuals.
Degree	…the number *and* strength of connections (or of given connections, for directed networks).	…are very close to, or give many interactions to, many individuals, but will have an even higher score if the connections are strong.
Instrength	…the strength of received connection.	…receive many interactions.
Indegree	…the number *and* strength of received connections.	…receive interactions from many individuals, but will have an even higher score if they receive many interactions.
Betweenness	…the individual's importance as a connection broker.	…are the bridge connecting many individuals either spatially or through interactions.
Clustering coefficient	…the number and strength of well connected neighbours.	…are close to many neighbours that are also close to each other, or interact with individuals who also interact with each other.

5.3. Results

A total of 12 takhi at Seer (8 colts and 4 fillies) and 14 takhi at Hustai (7 colts and 7 fillies) were incorporated in the juvenile SNA.

A count of the intragroup and intergroup agonistic and affiliative interactions occurring between juvenile takhi overall is shown in Table 5.2. Affiliative interactions were much more common among juvenile peers than were agonistic interactions. Play occurred more often at Seer than at Hustai. At Seer, charge, chase, and play interactions occurred more often between members of different groups, while head threats occurred more often between members of the same group. Mutual grooming was exclusively an intragroup interaction.

Table 5.2. Count of interaction occurrences at Seer and Hustai involving only juvenile takhi, broken down by type and intragroup and intergroup occurrence.

Location		Interaction	Intra	Inter	Overall
Seer	Agonistic	**Total**	**39**	**33**	**72**
		Charge	4	6	10
		Chase	0	1	1
		Head threat	35	26	61
	Affiliative	**Total**	**140**	**127**	**267**
		Mutual grooming	32	0	32
		Play	108	127	235
Hustai	Agonistic	**Total**	**10**		**10**
		Charge	0		0
		Chase	0		0
		Head threat	10		10
	Affiliative	**Total**	**39**		**39**
		Mutual grooming	34		34
		Play	5		5

5.3.1. Significant differences in juvenile centrality relative to group membership

As with adults (Chapter 4, section 4.3.1), CRG juveniles had significantly greater strength and degree than other groups in the intergroup spatial networks, while juveniles from BRG and DIG had higher intergroup cluster values (Table 5.3).

Significant trends relative to group membership were not observed in intergroup agonistic and affiliative networks at Seer.

Juveniles in DIG had significantly greater strength, degree, instrength, and cluster scores in intragroup affiliative networks than peers in other groups. This is probably because DIG had more juveniles, and particularly more colts, than any other family group. At Hustai, members of DNG had significantly greater strength, degree, instrength, and indegree than the juveniles in other focal groups.

There were no significant trends relative to group membership in juvenile intragroup spatial networks or agonistic networks at Seer or Hustai.

Table 5.3. Significant pairwise differences in spatial, agonistic, and affiliative network metrics among juveniles relative to group membership at Seer and Hustai. *ns* indicated no significant differences were detected in that network. *NA* indicates no tests were performed for that study site.

Location	Scale	Network	Metric	Group(s)…		…group(s)
Seer	Inter	Spatial	Strength	CRG…	…had significantly greater metric values than…	...BRG, DIG
			Degree	CRG…		...BRG
			Cluster	BRG…		...CRG
				DIG…		...BRG, CRG
		Agonistic	*ns*			
		Affiliative	*ns*			
	Intra	Spatial	*ns*			
		Agonistic	Cluster	CRG…		…DIG
		Affiliative	Strength	DIG…		...BRG, CRG
			Degree	DIG…		...BRG, CRG
			Instrength	DIG…		...BRG, CRG
			Cluster	DIG…		...BRG, CRG
Hustai	Inter	*NA*				
	Intra	Spatial	*ns*			
		Agonistic	*ns*			
		Affiliative	Strength/Degree	DNG…		...BDG, KEG, WNG, ZRG
			Instrength/Indegree	DNG…		...BDG, KEG, WNG, ZRG
			Cluster	BDG, DNG…		...KEG, WNG, ZRG

Location: Field site.

Scale: If 'Inter' the network only deals with intergroup links, if 'Intra' the network only deals with intragroup links.

Network: The spatial or interaction network for which metrics were calculated.

Metric: Network metric for which significant difference is being tested (see definitions overview in section 5.2.1).

5.3.2. Significant differences in juvenile centrality relative to sex

No significant differences in intragroup network centrality (at Seer and Hustai), and intergroup spatial and agonistic network centrality were detected (at Seer) relative to sex (Table 5.4). In the intergroup affiliative network, colts had significantly greater degree, instrength, and indegree than fillies. Colts tended to interact affiliatively with a greater number of individuals, and received more interactions and from more individuals than did fillies.

Table 5.4. Significant pairwise differences in spatial, agonistic, and affiliative network metrics among juveniles relative to sex at Seer and Hustai. *ns* indicates no significant differences were detected in that network.

Location	Scale	Network	Metric	Group(s)…	**…had significantly greater metric values than…**	…group(s)
Seer	Inter	Spatial	*ns*			
		Agonistic	*ns*			
		Affiliative	Degree	Colts…		...fillies
			Instrength/ Indegree	Colts…		...fillies
	Intra	*ns*				
Hustai	*ns*					

Location: Field site.

Scale: If 'Inter' the network only deals with intergroup links, if 'Intra' the network only deals with intragroup links.

Network: The spatial or interaction network for which metrics were calculated.

Metric: Network metric for which significant difference is being tested (see definitions overview in section 5.2.1).

5.3.3. Significant differences in juvenile centrality relative to personality (Seer only)

Trends in centrality relative to personality were related to group membership and sex (Table 5.5). The high centrality of social and mildly antisocial individuals was related to the high centrality of CRG members, who had very high strength and degree scores. However, mildly social individuals tended to have lower strength and degree values than social and mildly antisocial takhi from other groups as well. In the affiliative intergroup network, social and mildly social individuals had significant greater strength, degree, instrength, and indegree than mildly antisocial takhi. This trend appeared related to sex. Of the four fillies, three were mildly antisocial and one was mildly social, and this last was the only one connected in the network. All but one of the colts had social or mildly social personality scores, and all colts but one (classified as mildly social) were connected in the affiliative intergroup network.

There was no significant difference in intragroup network centrality relative to personality. There was no significant trend in network centrality relative to assertiveness score in juvenile takhi relationship networks.

Table 5.5. Significant pairwise differences in spatial, agonistic, and affiliative network metrics among juveniles relative to personality at Seer. ***ns*** **indicates no significant differences were detected in that network.**

Scale	Network	Metric	Attribute	Personality class(es)…	…had significantly greater metric values than…	…personality class(es)
Inter	Spatial	Strength/Degree	Sociable	Social, mildly antisocial…		...mildly social
	Agonistic	*ns*				
	Affiliative	Strength/Degree	Sociable	Social, mildly social…		...mildly antisocial
		Instrength/Indegree	Sociable	Social, mildly social…		...mildly antisocial
Intra	*ns*					

Network: The spatial or interaction network for which metrics were calculated.

Scale: If 'Inter' the network only deals with intergroup links, if 'Intra' the network only deals with intragroup links.

Metric: Network metric for which significant difference is being tested (see definitions overview in section 5.2.1).

Attribute: Personality trait for which a significant difference in metrics is being tested.

Season: Study period (see section 3.2.1.1 for exact dates). NB = non-breeding season and B = breeding season.

5.3.4. Summary of results

The strongest and most consistent results observed in these analyses were the continued centrality of CRG in intergroup spatial networks and the centrality of colts in intergroup affiliative networks at Seer. Members of DIG tended to be central in intragroup affiliative networks because that group had the most juveniles and the most colts.

In intergroup networks, colts interacted affiliatively with a greater number of individuals, and received more interactions and from more individuals than did fillies.

Trends in centrality relative to personality at Seer appeared related to observed trends in group membership and sex. Social and mildly antisocial individuals with high centrality in the intergroup spatial networks were members of CRG, and the social and mildly social individuals central in intergroup affiliative networks were primarily colts, while mildly antisocial individuals were fillies.

No spatial trends at Hustai were observed, and significant relationships in affiliative networks were based on the high occurrence of mutual grooming in the DNG group. Data were too sparse to confirm whether high grooming in DNG represented a trend or chance occurrence.

5.4. Discussion

Overall, significant differences in centrality relative to individual characteristics were often detected in juvenile intergroup networks, but only once in intragroup networks. Thus, individual characteristics such as group membership and sex were more strongly related to intergroup centrality than intragroup centrality.

5.4.1. The intergroup centrality of CRG

The centrality of CRG juveniles in intergroup spatial networks (Figure 5.1a) was related to the central position of the adults of the group, as group members of all ages travel together. Potential reasons for the spatial centrality of CRG were discussed in Chapter 4, section 4.4.1. Although equine juveniles older than one year do contribute to movement decisions in equid family groups (Bourjade and Sueur 2010, Krueger et al. 2014), it is improbable that the decisions of juveniles drove the spatial positioning of the CRG family group. It is more probable that CRG juveniles followed adults closer to other groups. It would be interesting to assess whether post-dispersal CRG juveniles continue to show higher centrality in intergroup spatial networks, or if they instead adapt the spatial patterning of the group that they join.

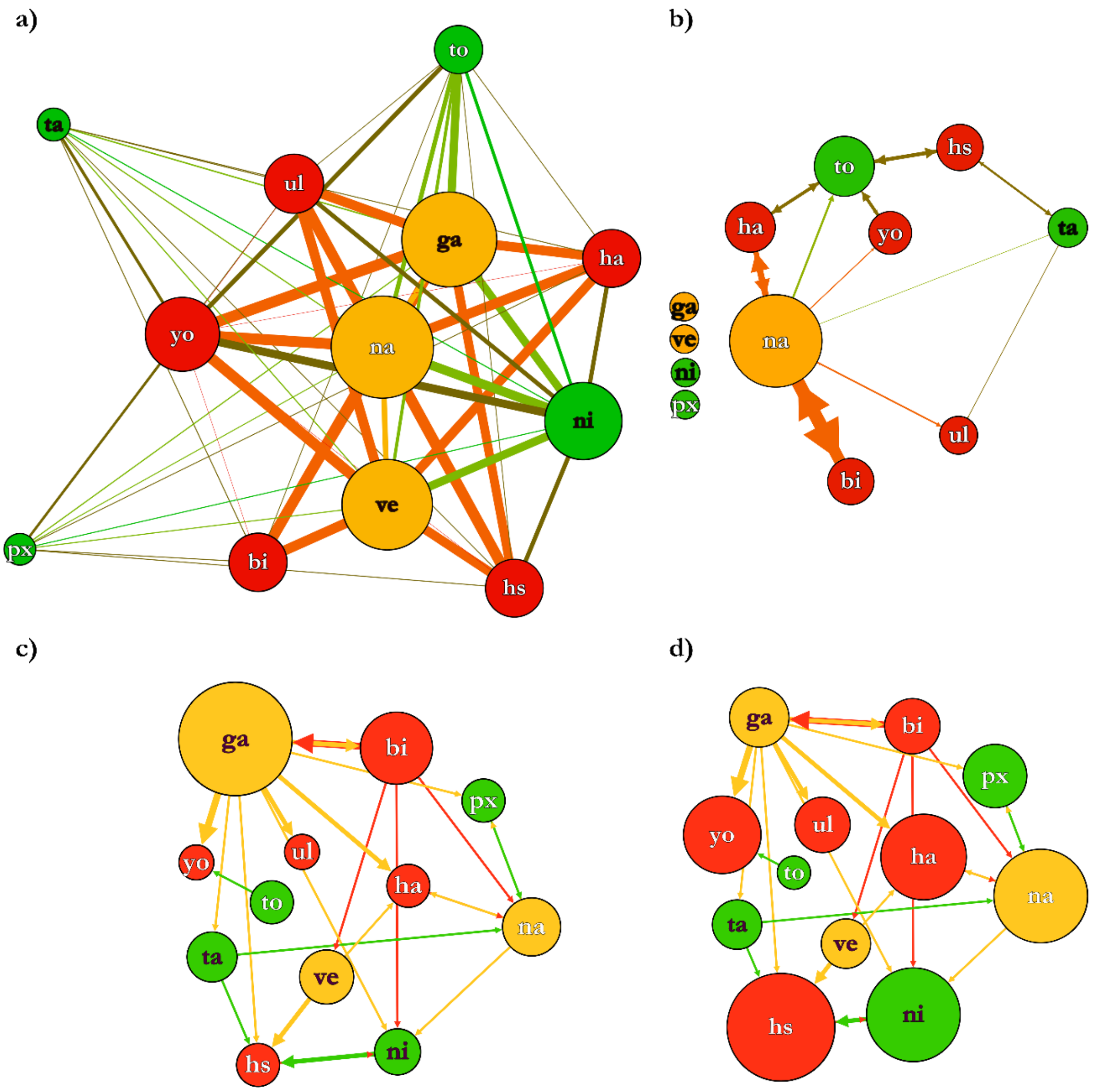


Figure 5.1. Sociograms showing the Seer juvenile intergroup (a) spatial network, (b) affiliative network, and (c and d) agonistic networks. Node size represents network strength (a), network degree (b and c) and network indegree (d). Node colour represents group membership; green = BRG, yellow = CRG, and red = DIG. Label colour indicates sex; black = filly and white = colt.

The lone CRG colt, NA, received and gave (Figure 5.1b) the most intergroup affiliative interactions and interacted with the most individuals of all the juveniles. However, CRG as a group did not have significantly greater intergroup affiliative centrality because the other two CRG juveniles, both fillies, were not connected in the intergroup network (Figure 5.1b). No significant difference in centrality by group was detected in the intergroup agonistic networks, but both CRG fillies, and particularly GA, the oldest of the juveniles, had the highest strength and degree (Figure 5.1c), and NA received agonistic interactions from a greater number of individuals than any other juvenile (Figure 5.1d). GA's agonistic interactions were directed at the oldest colts in the other groups (Figure 5.1c). While the differences in metric score between groups were not significant, the spatial centrality of CRG as a group may have put CRG juveniles in a position which provided them with more opportunities to interact with peers from other groups, both affiliatively and agonistically.

In previous studies investigating the intergroup relationships of Type I equids (Feist and McCullough 1976, Berger 1977, Miller and Denniston 1979, Rubenstein 1981, Berger 1986, Berger and Cunningham 1987, Monard et al. 1996, Linklater et al. 1999, Tong et al. 2015), intergroup juvenile relationships have only rarely been observed and then only affiliative interactions were reported (Berger 1986, Monard et al. 1996). Studies investigating agonistic intergroup interactions tended to focus on adult, or adult/juvenile exchanges, rather than those between juveniles (Berger 1977, Feist and McCullough 1976, Miller and Denniston 1979, Rubenstein 1981, Berger 1986, Berger and Cunningham 1987, Monard et al. 1996, Linklater et al. 1999, Tong et al. 2015). The intergroup relationships, particularly affiliative interactions, observed at Seer may only have occurred because adults, particularly stallions, were tolerant of the close proximity of other groups. However, the resulting increase in familiarity between juveniles from different groups may contribute to increased tolerance of proximity to other groups as juveniles mature. Further research should look at the relationship between the frequency of intergroup interactions as juveniles, particularly of affiliative interactions, and their tolerance of intergroup proximity as adults.

Overall, while juveniles were probably not active in causing the centrality of CRG in intergroup spatial networks, visual inspection of the affiliative and agonistic networks suggests that the spatial centrality of the group may have resulted in greater centrality in interaction networks, although the type of interactions in which individuals participated was largely dictated by sex (see section 5.4.2 for more discussion).

5.4.2. The intragroup centrality of DIG

The centrality of DIG in intragroup affiliative networks was the other significant difference in spatial centrality observed relative to group membership (Figure 5.2). DIG had the most juveniles, and all DIG juveniles were colts. Both CRG and BRG only had one and two colts, respectively, old enough to include in analysis. Intragroup play interactions occurred more often than mutual grooming (Table 5.2). Most studies have reported more play and grooming interactions occurring within groups than between groups (Feist and McCullough 1976, Wells and Goldschmidt-Rothschild 1979, Monard et al. 1996) and most reported more play among colts than fillies (Boyd 1988a, Sigurjónsdóttir et al. 2003, King et al. 2016). The presence of more juveniles in DIG, all of them colts, than in the other two groups, combined with the high occurrence of intragroup play, is enough to explain the significantly greater centrality of DIG in juvenile intragroup affiliative networks.

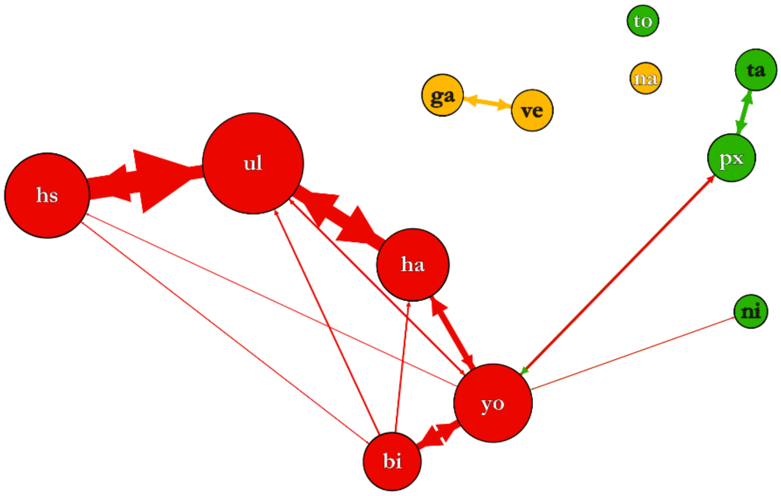


Figure 5.2. Sociogram showing the Seer juvenile intragroup affiliative network. Node size represents network strength and colour represents group membership; green = BRG, yellow = CRG, and red = DIG. Label colour indicates sex; black = filly and white = colt.

5.4.3. Differences in intergroup and intragroup centrality relative to sex

Significant differences in centrality relative to sex were detected in the Seer intergroup affiliative networks, where colts had greater degree (Figure 5.1b), indegree, and instrength than fillies. Differences relative to sex were not detected in intragroup networks. Fillies were inactive in intergroup affiliative networks (Figure 5.1b) but were more active in intragroup affiliative networks (Figure 5.2).

Fillies were involved in most of the intragroup mutual grooming interactions (22 out of 32), but only with one partner; GA and VE together, TA with PX, and NI with YO (Figure 5.2). TA was the only filly observed to engage in play, and then only intergroup (Figure 5.1b). Thus, engagement in mutual grooming boosted the centrality of fillies in the intragroup affiliative network, while colts engaged in all the intragroup play interactions. Crowell-Davis et al. (1986) found that filly foals groomed more than colt foals, and had less of a partner sex preference than colts, although fillies did show a slight preference for other fillies as partners. Crowell-Davis et al. (1986) proposed that these patterns of grooming preferences were practise for forming stronger female-female bonds later in life. Monard et al. (1996) found that fillies tended to have up to three preferred partners for affiliative interactions, usually their mother or matrilineal siblings. All fillies included in this study dispersed by the end of the study period. The full sisters GA and VE moved together to BRG, while the half-sisters TA and NI dispersed separately, although both eventually joined the same OTHER group.

Mare relationships are more often maintained passively through proximity maintenance (Wells and Goldschmidt-Rothschild 1979, van Dierendonck et al. 1995, 2004), although in the absence of a stallion, mares engage more in mutual grooming (Sigurjónsdóttir et al. 2003). Mutual grooming thus may serve as a backup mechanism for maintaining stable relationships and group cohesion, when no stallion is present to actively maintain group borders. The higher occurrence of mutual grooming between filly foals (Crowell-Davis et al. 1986), and between the pre-dispersal fillies at Seer may represent social practise in relationship formation and maintenance in the same manner as the play between colts.

Significantly greater affiliative intragroup, as well as intergroup, network centrality in colts was not observed because the colts of BRG and CRG had only one or no same-sex peers available as playmates and fillies tend to play less with conspecifics than do colts (Boyd 1988a, Sigurjónsdóttir et al. 2003, Cameron et al. 2008, King et al. 2016). As no intergroup mutual grooming occurred, intergroup links represented only play interactions. Thus, colts were significantly central in networks which included only play interactions (Figure 5.1b), but not significantly central in the intragroup networks where mutual grooming also occurred, although the DIG colts were well connected in the intragroup network by play interactions. Stanley and Shultz (2012) found that colts, but not fillies, showed a significant increase in spatial centrality as they matured. Colts had an increasing number of associates as they grew older, while the number of associates for fillies remained constant (Stanley and Shultz 2012). Monard et al. (1996) also found that fillies tended to have few social partners, but strong bonds with those they did have. This study did not follow changes in associations over time, but did find that colts had a greater variety of partners for affiliative interactions than fillies. This study did not detect significant differences in spatial association relative to sex.

Intergroup interactions, particularly play, give colts contact with a greater variety of individuals with different interaction styles, and give them experience engaging in real and mock versions of both affiliative and agonistic interactions. Social experience gained as juveniles can be key to later success as adults, first in integrating into a bachelor group and later in forming a family group (Stanley and Shultz 2012). Social experience and practise for colts is particularly important as stallion success in intraspecific confrontations is based more on skill and ability than on size (Berger 1986, Stanley and Shultz 2012). Play can also be a low risk method for deciding questions of dominance (Goodwin and Hughes 2005) and can thus potentially reduce the frequency and severity of more agonistic encounters with bachelors and family stallions post-dispersal. Thus, the greater centrality of colts in the Seer intergroup affiliative networks is due to their taking advantage of the social shelter provided by the family group and herd structure to develop and practise physical and social skills with additional partners in a relatively low risk environment (Stanley and Shultz 2012).

The intergroup affiliative connections observed at Seer between juveniles, and particularly colts, may only have occurred because stallions were tolerant of the close proximity of other groups (as discussed in Chapter 4 and more in Chapter 6), but the resulting increase in familiarity with playmates from different groups may contribute to increased tolerance of proximity to other groups among stallions once the same colts reach maturity. Further research should look at the relationship between frequency of intergroup play as a juvenile and tolerance of intergroup proximity as an adult stallion in a family group.

5.4.4. Personality trends

Centrality trends relative to personality in the intergroup spatial and affiliative networks were related to the trends in group membership and sex already discussed. In the intergroup spatial network, CRG members were significantly central and were classed as social and mildly antisocial (Figure 5.3a). However, social and mildly antisocial individuals who were not members of CRG were also more central than mildly social juveniles, who occupied very peripheral positions in the network (Figure 5.3a).

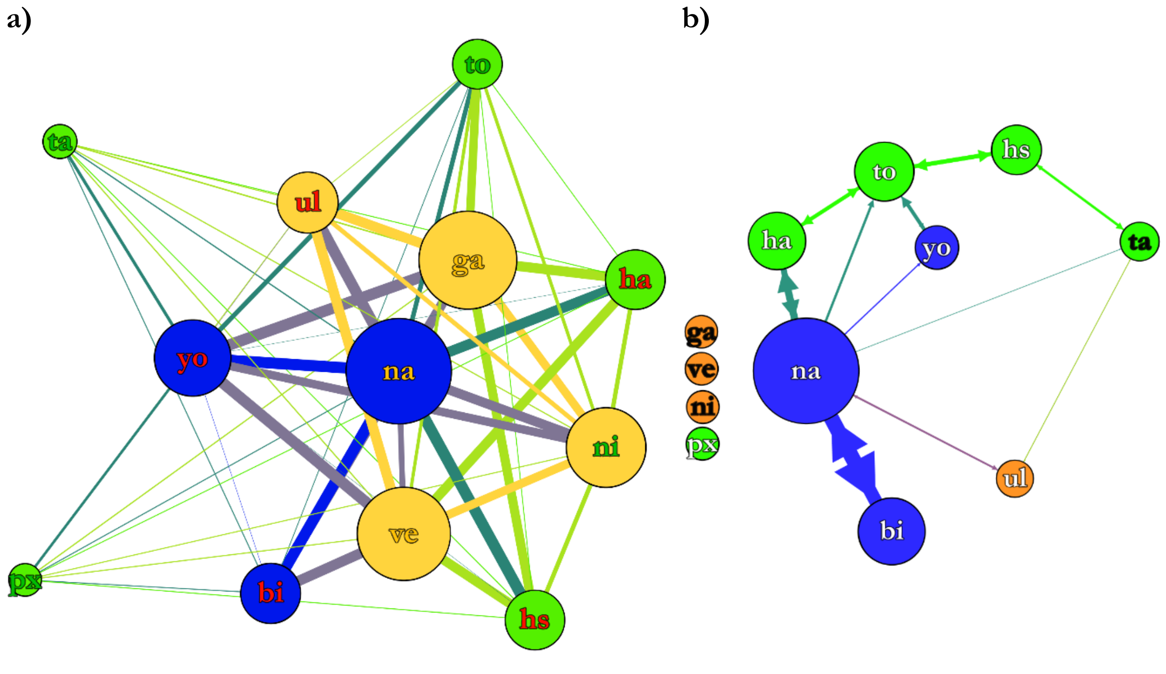


Figure 5.3. Sociograms showing Seer juvenile (a) spatial and (b) affiliative intergroup networks. Node size represents network strength and colour represents personality; blue = social, green = mildly social, and yellow = mildly antisocial. Label colour for (a) indicates group; green = BRG, yellow = CRG, and red = DIG. Label colour for (b) indicates sex; black = filly and white = colt.

Other research on the influence of personality on cohesion reported more linear relationships between personality and cohesion than were observed at Seer. In the context of a single social group, Briard et al. (2015) predicted that less gregarious (social) individuals would be more bold and more likely to move away from a group of conspecifics, as was seen in sheep (Sibbald et al. 2009), while more gregarious individuals would be less bold and stay close to conspecifics. Nuñez et al. (2015) found more spatially central juveniles (which the authors described as more social) were more likely to survive separation from some or all of their natal group than were less social individuals. At Seer in both juvenile and adult spatial networks, individuals classed as mildly social tended to be more peripheral, while individuals who were more and less social than the mildly social individuals were more central, resulting in a non-linear relationship between spatial centrality and sociability. Further research should investigate why raters assessed certain individuals as mildly social, and whether the tendency for mildly social individuals to be more peripheral is repeatable across time in this population or can be found in other takhi populations. If results are consistent, sociability could prove to be a predictor of cohesive tendency in takhi.

The greater centrality of social and mildly social individuals in the intergroup affiliative networks appeared strongly related to sex (see Figure 5.3b). As was discussed in Chapter 2, males tended to have higher sociability scores than females. When results were broken down by reproductive state the difference in score was only significant between lactating mares and colts, but there was a tendency for colts to have higher sociability scores than all other reproductive classes, including fillies (see Chapter 2, Figure 2.3a). Of the fillies included in analysis, three were classed as mildly antisocial and one was classed as mildly social, while three colts were classed as social, four as mildly social, and only one as mildly antisocial (Figure 5.3b). More social individuals and more colts were more central in the intergroup affiliative network (Figure 5.3b), so differences in centrality relative to personality in the affiliative intergroup network were directly related to the sex of the individuals.

5.4.5. Hustai trends

The only network at Hustai where a significant difference in centrality was detected was the intragroup affiliative network. Most of the affiliative interactions observed were mutual grooming (Table 5.2) and most were observed in the spring. DNG was observed for one day in spring during which all group members engaged in frequent mutual grooming interactions. The high centrality of DNG in the affiliative network was due to the high rate of mutual grooming on that day. Further research would be necessary to determine whether the high affiliative centrality of DNG had any cause beyond the high activity of the group during the May observation period.

5.5. Chapter Outcomes

The purpose of this chapter was to assess whether the group membership, reproductive state, or personality of juvenile takhi influenced their centrality in intragroup and intergroup spatial, agonistic, and affiliative networks.

Main chapter findings were as follows:

- As was observed with adults, juvenile members of CRG were significantly more central than members of BRG and DIG in the intergroup spatial network, but their centrality probably does not represent an independent tendency of the CRG juveniles to be closer to the members of other groups. Rather, juveniles travelling with the adults of CRG together as a group were spatially central in the herd.
- Members of DIG were significantly more central in intragroup affiliative networks because DIG contained five colts who played together frequently.
- Colts were significantly more active than fillies in intergroup affiliative networks because they engaged in frequent play sessions with colts from other groups.
- Juveniles of both sexes were more equal in intragroup affiliative activity, but fillies tended to groom with peers and colts played with peers.
- Mildly social individuals tended to be peripheral in intergroup spatial networks. The trend was related to the centrality of the social and mildly antisocial members of CRG, but not completely explained by it.

The next results chapter will investigate whether group membership, reproductive state, and personality had a significant influence on cross age relationships between adults and juveniles (Chapter 6) in intragroup and intergroup spatial, agonistic, and affiliative networks.

6. Adult/juvenile cross age class relationships: the influence of individual characteristics on the relationships between adult and juvenile takhi in intragroup and intergroup spatial, agonistic, and affiliative networks

6.1. Introduction

This chapter will explore the remaining two of the four types of takhi family group relationships first described in Chapter 4, section 4.1. Chapter 4 looked at factors influencing the relationships between adult peers. Chapter 5 explored factors influencing the relationships of pre-dispersal juvenile peers. This chapter will investigate factors influencing the relationships between adult takhi and pre-dispersal juveniles who have reached nutritional independence (Stanley and Shultz 2012). Cross age class relationships include ties between parents and offspring, and between adults and familiar, non-offspring juveniles.

Cross age class relationships are an important part of family group social structure, as the production of a younger generation which survives and itself reproduces is the fundamental purpose of family group formation. The young of social species such as takhi need a relatively extensive period, even beyond nutritional independence, in which to learn from adults and develop with peers the social skills necessary to be successful as an adult (Dunbar 1998, Stanley and Shultz 2012). However, the structure of family groups, with one stallion and multiple mares with their own offspring, results in changes in the costs and benefits for the individuals co-occurring in the group as juveniles mature.

Dams want their offspring to be successful. For their offspring to be so they need to be strong and healthy (Trivers and Willard 1973, Cameron et al. 2008), and they also need to be socially competent (Berger 1986, Cameron et al. 2008, Stanley and Shultz 2012). As was discussed in Chapter 5, section 5.4.3, this is particularly important for colts. Stanley and Shultz (2012) found that dams were more active in maintaining affiliative bonds with their sons than their daughters. The authors proposed that this was an effort to balance the greater agonistic pressure from the family stallion and other adult mares in the group. Dams also need to provide for younger offspring and maintain their own condition (Feist and McCullough 1976, Duncan et al. 1984) and as a result the offspring of pregnant mares tend to be weaned sooner than non-pregnant mares (Duncan et al. 1984, King et al. 2016). Juveniles typically stay in their natal group until they are two to three years old, although some may stay until they are as old as five (Monard et al. 1996, Khalil and Kaseda 1998, Boyd and Keiper 2005). Thus, there are usually at least one or two younger full-siblings present in the same group. As new foals are born, the presence of older offspring may begin to represent more of a cost to their dams, as a physical risk to the younger sibling (Boyd 1988a) and as sharerers of resources needed by the younger foal if the older juveniles are not yet weaned (Feist and McCullough 1976). Stanley and Shultz (2012) argue that suckling by juveniles over one year is primarily non-nutritive and so probably does not represent a significant cost to the mare. Matrilineal subfamilies, consisting of a mare, her foal of the year, and any pre-dispersal offspring, often form clear social subgroups in families, within which the majority of intragroup affiliative interactions occur (Wells and Goldschmidt-Rothschild 1979).

The other mares of the family group have the least invested in the juveniles of their peers, but equid feeding habits are such that neither are they in direct conflict with them unless resources are very scarce and patchy. Although competition over resources among group and herd members is possible in areas with more restricted resource access (Rubenstein 1981, 1994) mares and older juveniles can generally distribute themselves within groups and herds in a way that minimises competition over grazing and access to water (Rubenstein 1994, Tong et al. 2015). Older juveniles do present a potential physical risk to the young foals of other lactating mares in the group (Boyd 1988a, Stanley and Shultz 2012), and older colts may harass adult mares during the breeding season (Davie pers obs, Stanley and Shultz 2012). However, the presence of other adult mares can also have a potential benefit for the social learning and social integration of juveniles. Bourjade et al. (2009) found that higher proportions of adults to juveniles in groups of takhi were correlated with lower rates of aggression and less social segregation among juveniles.

Sires also want their offspring to be successful. They primarily invest in juveniles by keeping them safe from conspecifics and predators (Berger 1986, Klimov 1988, Rubenstein 1994) and providing social education by playing and interacting with them, especially with colts (Berger 1986, Feh 1988, Kaseda and Khalil 1996, Cameron et al. 2008, King et al. 2016). As juveniles reach dispersal age their relationship with the stallion begins to change. Fillies avoid mating with their father, and often the reverse is true (Berger and Cunningham 1987, Monard et al. 1996), but sometimes the intervention of the family mares is necessary to prevent the harassment of a filly by her father (Monard et al. 1996). Stallions will sometimes ignore courting and mating between their daughters and other family stallions and bachelors (Monard et al. 1996), but at other times will attempt to herd the filly back to the family group. Colts are also met with varying degrees of tolerance by stallions. As colts mature they become more socially active (Stanley and Shultz 2012) and they may begin to harass other mares in the group, especially during the breeding season (Davie pers obs, Stanley and Shultz 2012), which can be disruptive to the group overall. Because the breeding season overlaps with foaling season (Rubenstein 1994, King 2002, Ransom et al. 2016), it also presents a severe risk to new foals, who can easily be trampled in within and between group scuffles (Boyd 1988a, Feh 1999). Up to a point, continuing to protect his sons as they mature physically and socially benefits the stallion. However, if they being to disrupt the social group too much, the costs begin to outweigh the benefits of any additional investment. Most colts and fillies leave their natal group voluntarily (Tyler 1972, Rutberg and Keiper 1993, Monard et al. 1996, Khalil and Kaseda 1998). As juveniles get older their sire will sometimes direct more aggressive interactions toward them (Stanley and Shultz 2012) and may actively drive them out of the group if they do not leave on their own (Tyler 1972, Klingel 1975, Feh 1999).

Older juveniles, particularly colts, appear to take advantage of the social shelter provided by the family group and the presence of their parents to continue to develop physically and socially in a relatively low risk environment even after having reached nutritional independence (Stanley and Shultz 2012). While still in the group, colts can practise affiliative social skills and learn to apply agonistic ones effectively (Duncan et al. 1984, Berger 1986, Stanley and Shultz 2012). For juveniles of both sexes, it would be ideal to stay with their natal group until they are ready to reproduce, and this is usually what happens with fillies. Fillies tended wait to disperse until or after they reached first oestrus (Monard et al. 1996). Monard et al. (1996) found no evidence of increased aggression or reduced sociality in fillies prior to dispersal and concluded that filly dispersal was driven by attraction to non-group males, not repulsion by members of their natal group or competition with adult mares for resources. Colts are more apt to experience both natal group repulsion and attraction to non-group members (Khalil and Kaseda 1998). Juveniles disperse when social costs outweigh the benefits of remaining in their natal group. For fillies, the primary cost of not dispersing is the risk of incest (Monard et al. 1996), while for colts the primary cost is increased conflict with adults and lack of access to breeding partners (Berger 1986, Stanley and Shultz 2012).

From the literature, it was expected that reproductive state will have the strongest influence on the centrality of individuals in adult/juvenile networks. Some studies have found a significant difference in the giving and receiving of affiliative and agonistic interactions depending on the reproductive state and relationship history of interacting individuals (Wells and Goldschmidt-Rothschild 1979, King et al. 2016), while other studies have found no difference in the frequency and levels of interaction among group members of different age and reproductive state (Krueger et al. 2014).

No studies in the literature were found which investigated the role of personality in shaping adult/juvenile relationships in natural social groups. Baker (2015) tested separately for and found significant relationships between age and personality and sex and personality in the Le Villaret takhi population, but did not explore the influence of the relationship between sex, age, and personality on interindividual interactions. Bouskila et al. (2015) acknowledged the probability that individual variation in personality has an important role in shaping group structure, but also highlighted the need for dependable and consistent methodology for assessing personality in free-living individuals. This chapter will continue to explore the potential influence of individual personality on intra- and intergroup relationships using the personality scores developed in Chapter 2. Studies with other species have documented the impact of personality on dominance, dispersal tendencies, and stress (Bremner-Harrison et al. 2004, Reale et al. 2007), all of which play a role in adult/juvenile relationships.

Group membership could also have an influence on cross age relationships. Less confident stallions are more apt to move their group around when other groups are present (Rubenstein 1994). Constant minding and harassment will influence the well-being of mares and their offspring (Rubenstein 1994, Feh 1999, Linklater et al. 1999) and could thus impact interindividual relationships with the stallion and between mares and juveniles. The rank of the stallion can have a greater influence on mare reproductive success than the mare's own rank within the family group, and mares with higher ranking stallions were found to gain up to six minutes per hour of grazing time (Rubenstein 1994). Less grazing time could make mares more aggressive towards juveniles who get in the way while they are eating. More frequent spatial management by the stallion could also increase risk to young foals, as frequent and aggressive herding can be disruptive and dangerous. Group size can also influence the relationships of individuals in the group. Ransom et al. (2010) found a small (0.7%) but significant decrease in agonistic (but not affiliative) interactions with an increase in group size, but did not suggest an explanation for the observed relationship. Rubenstein (1994) reported a similar trend. Miller and Denniston (1979) found a significant positive correlation between group dominance and group size.

This chapter will investigate potential behavioural mechanisms promoting intra- and intergroup cohesive behaviour between adult and juvenile takhi at Seer and Hustai by identifying significant trends in the relationships between the group membership, reproductive state, and personality of individuals and their importance in spatial, agonistic, and affiliative intragroup and intergroup networks. The aim of the chapter is to identify individuals with a central role in maintaining spatial and social connections between adult and juvenile takhi within and between family groups.

6.2. Methods

The purpose of this portion of the analysis was to determine whether adult/juvenile cross age class relationships were influenced by group membership, reproductive state, or personality. All individuals included in Chapter 4 and Chapter 5 analyses were included in the SNA in this chapter. Spatial, agonistic, and affiliative networks only included links that connected an adult to a juvenile and vice versa. Networks were divided into intragroup and intergroup networks, and into non-breeding and breeding seasons (see Chapter 3, section 3.2.1.1 for season definitions). Spatial, agonistic, and affiliative networks and all attribute data were assembled using the methods described in Chapter 3, section 3.2.3.

6.2.1. Review of network metrics interpretation

Presented below are the results of tests for a significant difference in centrality among individuals using several network metrics. The summary table from Chapter 3, section 3.1.2.4 (Table 3.1) defining and interpreting each network metric is reproduced below for ease of reference within the chapter (Table 6.1). Further definitions of network terminology can be found in the glossary in Chapter 3, Appendix 3.I.

Table 6.1. A summary of how the network metrics applied in this study are interpreted in the context of spatial and interaction networks.

Network metric	Measures…	Individuals with a high score…
Strength	…the strength of connections (or of given connections, for directed networks).	…are very close to, or give many interactions to, a few or many individuals.
Degree	…the number *and* strength of connections (or of given connections, for directed networks).	…are very close to, or give many interactions to, many individuals, but will have an even higher score if the connections are strong.
Instrength	…the strength of received connection.	…receive many interactions.
Indegree	…the number *and* strength of received connections.	…receive interactions from many individuals, but will have an even higher score if they receive many interactions.
Betweenness	…the individual's importance as a connection broker.	…are the bridge connecting many individuals either spatially or through interactions.
Clustering coefficient	…the number and strength of well connected neighbours.	…are close to many neighbours that are also close to each other, or interact with individuals who also interact with each other.

6.3. Results

The ratio of adults to juveniles ranged between 1.5:1 to 3:1 in most focal family groups, although the ratio was as high as 6:1 in CRG in the breeding season and ZRG during the non-breeding season. Forty-two percent of all interactions observed at Seer and 53% of interactions at Hustai occurred between adults and juveniles.

A count of the intragroup and intergroup agonistic and affiliative interactions occurring between adults and juveniles is shown in Table 6.2. Charge and chase interactions tended to involve the members of different groups, while head threats tended to be intragroup. Play was almost strictly intergroup, and mutual grooming primarily intragroup, although it did occur between members of different groups during the non-breeding season at Seer.

Table 6.2. Count of interactions at Seer and Hustai occurring between adults and juveniles, broken down by type and intragroup and intergroup occurrence.

Location		Interaction	Non-breeding		Breeding		Total		
			Intra	Inter	Intra	Inter	Intra	Inter	Overall
Seer	Agonistic	**Total**	**100**	**88**	**78**	**51**	**178**	**139**	**317**
		Charge	17	26	10	10	27	36	**63**
		Chase	1	0	0	16	1	16	**17**
		Head threat	82	62	68	25	150	87	**237**
	Affiliative	**Total**	**37**	**226**	**13**	**27**	**50**	**253**	**303**
		Mutual grooming	34	12	12	0	46	12	**58**
		Play	3	214	1	27	4	241	**245**
Hustai	Agonistic	**Total**	**22**		**41**		**63**		**63**
		Charge	1		1		2		**2**
		Chase	0		1		1		**1**
		Head threat	21		39		60		**60**
	Affiliative	**Total**	**16**		**131**		**147**		**147**
		Mutual grooming	16		68		84		**84**
		Play	0		63		63		**63**

6.3.1. Significant differences in cross age centrality relative to group membership

There was a significant difference in cross age centrality relative to group membership in the intergroup spatial network, and intragroup affiliative network at Seer, and in the intragroup agonistic and affiliative networks at Hustai (Table 6.3).

The group OTHER had significantly lower strength than the other groups during the non-breeding season (degree as well) and breeding season, but this is to be expected, as members of OTHER tended to be far away from all other groups. During the non-breeding season, adults and juveniles of CRG had greater strength and degree than did members of DIG (Table 6.3). Members of CRG tended to be closer to, and closer to more, members of the opposite age class in other groups than were members of DIG.

Table 6.3. Significant pairwise differences in spatial, agonistic, and affiliative cross age network metrics relative to group membership at Seer and Hustai. *ns* indicated no significant differences were detected in that network. *NA* indicates no tests were performed for that study site.

Location	Scale	Network	Metric	Season	Group(s)…		…group(s)
Seer	Inter	Spatial	Strength	NB	CRG…	…had significantly greater metric values than…	…DIG
				NB	BRG, CRG, DIG…		…OTHER
				B	BRG, CRG…		…OTHER
			Degree	NB	CRG…		…DIG
				NB	BRG, CRG, DIG…		…OTHER
		Agonistic	*ns*				
		Affiliative	*ns*				
	Intra	Spatial	*ns*				
		Agonistic	*ns*				
		Affiliative	Instrength/Indegree	NB	BRG…		…DIG
Hustai	Inter	*NA*					
	Intra	Agonistic	Strength/Degree	B	DNG…		…BDG, ZRG
				B	WNG…		…BDG
		Affiliative	Betweenness	B	DNG…		…BDG, KEG, WNG, ZRG
			Strength/Degree	NB	BDG…		…DNG, WNG
				B	DNG…		…BDG, KEG, ZRG
				B	WNG…		…KEG
			Instrength/Indegree	NB	BDG…		…DNG, WNG
				B	DNG…		…BDG, KEG, ZRG
				B	WNG…		…KEG

Location: Field site.

Scale: If 'Inter' the network only deals with intergroup links, if 'Intra' the network only deals with intragroup links.

Network: The spatial or interaction network for which metrics were calculated.

Metric: Network metric for which significant difference is being tested (see definitions overview in section 6.2.1).

Season: Study period (see section 3.2.1.1 for exact dates). NB = non-breeding season and B = breeding season.

BRG had significantly greater instrength and indegree than DIG in the intragroup affiliative network in the non-breeding season (Table 6.3). Very few members of DIG engaged in cross age affiliative interactions, while almost all members of BRG engaged in affiliative interactions. The high instrength of BRG was primarily because TA, a filly who dispersed after the end of the season, engaged in mutual grooming with all but two of the adults in the group (Figure 6.1).

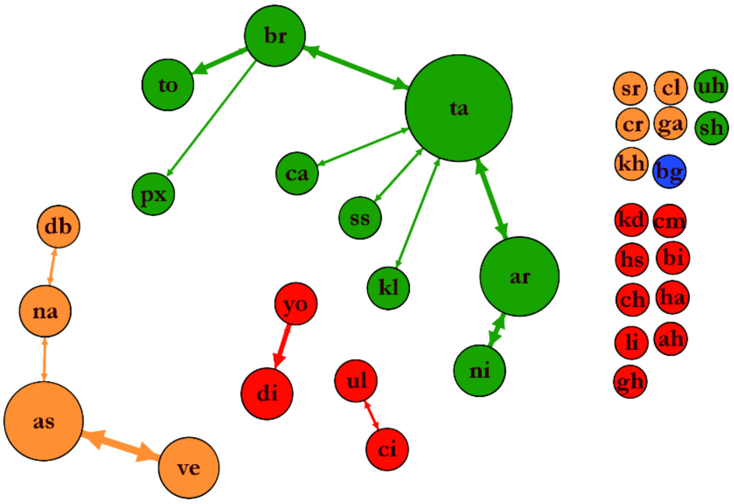


Figure 6.1. Sociogram showing the cross age Seer adult/juvenile intragroup affiliative network for the non-breeding season. Node size represents network instrength and colour represents group membership; green = BRG, yellow = CRG, red = DIG, and blue = OTHER.

In the non-breeding affiliative intragroup network at Hustai, BDG had significantly greater strength, degree, instrength, and indegree than DNG and WNG (Table 6.3). Several members of BDG engaged in affiliative interactions, while no members of either DNG or WNG did. In contrast, in the breeding season DNG had greater betweenness, strength, degree, instrength, and indegree than the other focal groups. WNG had greater strength, degree, instrength, and indegree than KEG. The members of DNG engaged in a lot of mutual grooming, especially during the May observation period. The stallion and one colt of WNG exchanged many play interactions, while no cross age affiliative interactions were exchanged between the members of KEG. DNG had significantly greater breeding season intragroup agonistic centrality than BDG and ZRG because all members of DNG engaged in cross class agonistic interactions, while only half of ZRG members did. ZRG also only had one juvenile member. WNG had greater strength and degree than BDG because all but one of WNG’s members was connected in the network, while only two members of BDG engaged in agonistic cross class interactions.

6.3.2. Significant differences in cross age centrality relative to reproductive state

There was a significant difference in network centrality relative to reproductive state in the non-breeding and breeding intergroup agonistic and affiliative networks at Seer (Table 6.4). At both Seer and Hustai there was a significant difference in centrality relative to reproductive state in the intragroup spatial and agonistic, but not affiliative, networks (Table 6.4).

Stallions were very active in Seer intergroup agonistic networks in both seasons, with significantly greater betweenness than mares, and significantly greater strength and degree than all other reproductive classes (Table 6.4). Non-lactating mares had greater strength and degree than colts and fillies in the non-breeding and breeding seasons. Lactating mares had greater strength and degree than colts but not fillies in both seasons. Colt and fillies had high betweenness because they tended to receive interactions from multiple individuals. They also had greater instrength and indegree than all adults during both seasons.

Stallions and colts received and gave significantly more cross age affiliative intergroup interactions than mares and fillies during the non-breeding season (Table 6.4). No significant trends were detected during the breeding season.

Table 6.4. Significant pairwise differences in spatial, agonistic, and affiliative cross age network metrics relative to reproductive state at Seer and Hustai. *ns* indicated no significant differences were detected in that network. *NA* indicates no tests were performed for that study site.

Location	Scale	Network	Metric	Season	Reproductive class(es)…		…reproductive class(es)
Seer	Inter	Spatial	*ns*			…had significantly greater metric values than…	
		Agonistic	Betweenness	NB	Stallions…		…all mares, colts
				NB	Colts, fillies…		…all mares
				B	Stallions, colts, fillies…		…lactating mares
				B	Stallions…		…nonlactating mares
			Strength/Degree	NB/B	Stallions…		…all mares, colts, fillies
				NB/B	Nonlactating mares…		…colts, fillies
				NB	Lactating mares…		…colts
			Degree	NB/B	Stallions…		…all mares, colts, fillies
				NB	All mares…		…colts
				B	Nonlactating mares…		…colts, fillies
			Instrength	NB	Colts, fillies…		…all adults
				B	Fillies…		…all adults, colts
				B	Colts…		…all adults
			Indegree	NB/B	Colts, fillies…		…all adults
		Affiliative	Strength/Degree	NB	Stallions, colts…		…all mares, fillies
			Instrength	NB	Stallions…		…lactating mares, fillies
				NB	Colts…		…all mares, fillies
			Indegree	NB	Stallions…		…lactating mares
				NB	Colts…		…all mares, fillies
	Intra	Spatial	Betweenness	NB	Colts…		…stallions
				NB	Fillies…		…all adults

			Strength	NB	Non-lactating mares…		…stallions
				NB	Fillies…		…all adults
				B	Colts…		…lactating mares, stallions
				B	Fillies…		…all adults, colts
		Agonistic	Strength/Degree	NB	All adults…		…colts
				NB	Lactating mares…		…fillies
				B	All mares…		…colts, fillies
				B	Non-lactating mares…		…stallions
			Instrength/Indegree	NB	Stallions, non-lactating mares…		…lactating mares
				NB	Colts…		…all adults
				NB	Fillies…		…all adults, colts
				B	Colts, fillies…		…all adults
		Affiliative	*ns*				
Hustai	Inter	*NA*					
	Intra	Spatial	Betweenness	NB	Lactating mares, colts, fillies…		…non-lactating mares, stallions
			Strength/Degree	NB	Lactating mares…		…non-lactating mares, stallions
				NB	Colts…		…all adults, fillies
				NB	Fillies…		…stallions
		Agonistic	Betweenness	B	Fillies…		…all adults, colts
			Instrength/Indegree	NB	Colts, fillies…		…lactating mares, stallions
				B	Fillies…		…all adults, colts
		Affiliative	*ns*				

Location: Field site.

Scale: If 'Inter' the network only deals with intergroup links, if 'Intra' the network only deals with intragroup links.

Network: The spatial or interaction network for which metrics were calculated.

Metric: Network metric for which significant difference is being tested (see definitions overview in section 6.2.1).

Season: Study period (see section 3.2.1.1 for exact dates). NB = non-breeding season and B = breeding season.

In the Seer non-breeding intragroup spatial network, colts had greater betweenness than stallions because multiple colts were connected to AR, who was connected to both BRG and DIG juveniles, and fillies had greater betweenness than all adult classes because TA had ties to BG and AR after her dispersal at the end of the non-breeding season, and NI of BRG also had close ties to AR (Figure 6.2). Non-lactating mares, primarily AR and BG, had greater strength than stallions, and fillies had greater strength than all adults (Table 6.4). In the intragroup spatial network colts had greater strength than lactating mares and stallions, and fillies had greater strength than all adults and colts. The higher strength of colts occurred because all lactating mares and stallions were in groups with more adults than juveniles. The high strength of fillies was because three fillies changed groups during the breeding season, and so had strong ties to the adults in two groups.

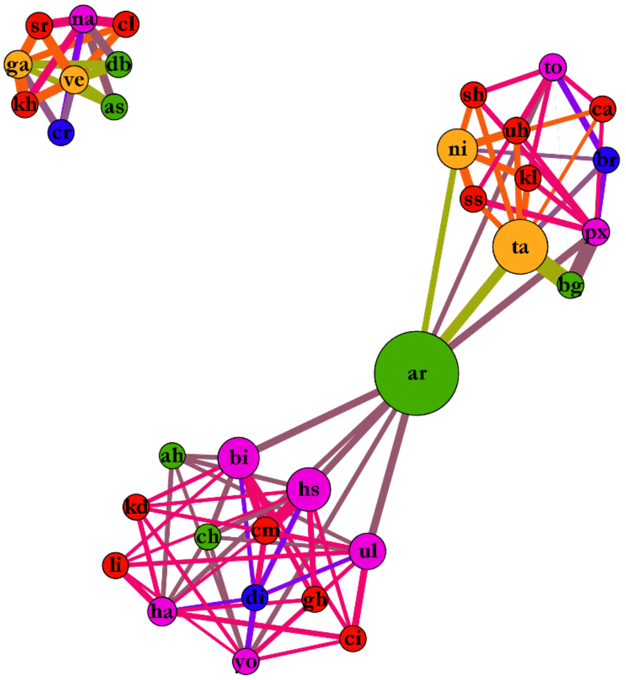


Figure 6.2. Sociogram showing the cross age Seer adult/juvenile intragroup spatial network for the non-breeding season. Node size represents network betweenness and colour represents reproductive state; blue = stallion, red = lactating mare, green = non-lactating mare, yellow = filly, and pink = colt.

In the intragroup agonistic networks at Seer during both the non-breeding and breeding season, mares, and particularly lactating mares, gave significantly more interactions than juveniles (Table 6.4). In the breeding season non-lactating mares gave significantly more interactions than stallions. In both seasons juveniles received significantly more agonistic interactions than did adults. In the non-breeding season stallions and non-lactating mares had greater instrength and indegree than lactating mares, as the former occasionally received agonistic interactions from juveniles (often fillies) but lactating mares did not. In the non-breeding season fillies received more agonistic interactions than did colts.

At Hustai, during the non-breeding season, lactating mares, colts, and fillies tended to have greater betweenness, strength, and degree than non-lactating mares and particularly stallions (Table 6.4). The high centrality appeared to be due to the tendency of dams and offspring to group together, while stallions and non-lactating mares were less apt to have close neighbours. In the non-breeding season juveniles of both sexes received significantly more agonistic interactions than lactating mares and stallions, and in the breeding season fillies received significantly more agonistic interactions than all adults and colts. Fillies also had greater betweenness than all adults and colts, as in KEG and DNG the fillies were at the centre of the agonistic network (Figure 6.3).

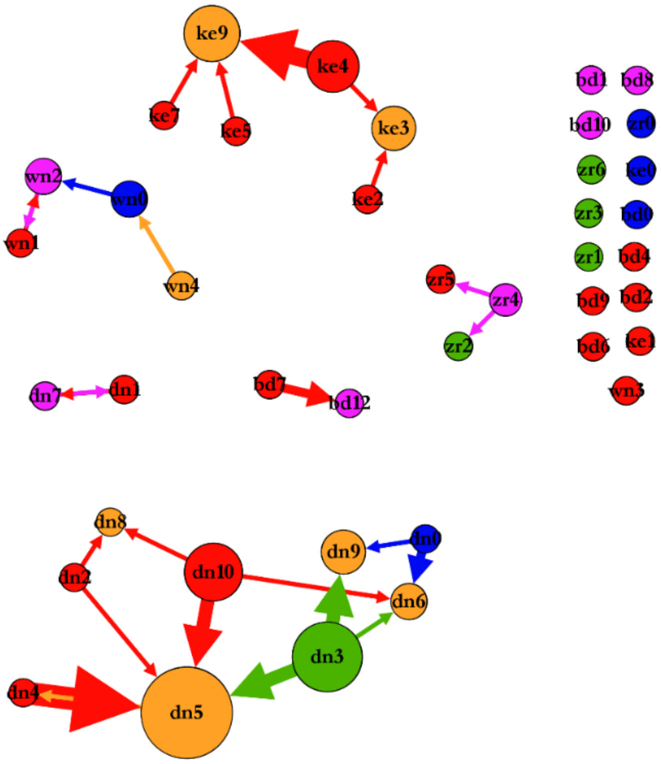


Figure 6.3. Sociogram showing the cross age Hustai adult/juvenile intragroup agonistic network for the breeding season. Node size represents network betweenness and colour represents reproductive state; blue = stallion, red = lactating mare, green = non-lactating mare, yellow = filly, and pink = colt.

6.3.3. Significant differences in cross age centrality relative to personality (Seer only)

At Seer, there was a significant difference in centrality relative to personality in intergroup spatial, agonistic, and affiliative networks and intragroup spatial and agonistic networks (Table 6.5).

Table 6.5. Significant pairwise differences in spatial, agonistic, and affiliative cross age network metrics relative to personality at Seer. *ns* indicated no significant differences were detected in that network.

Scale	Network	Metric	Attribute	Season	Personality class(es)…		…personality class(es)
Inter	Spatial	Betweenness	Sociable	NB	Social, mildly antisocial…	…had significantly greater metric values than…	…mildly social, antisocial, very antisocial
		Strength	Sociable	NB	Social, mildly antisocial…		…mildly social, antisocial, very antisocial
		Degree	Assertiveness	NB	Very assertive, mildly diffident...		…assertive, mildly assertive
				NB	Diffident…		…assertive
			Sociable	NB	Social, mildly antisocial…		…mildly social, antisocial, very antisocial
	Agonistic	Betweenness	Sociable	B	Social…		…mildly social, mildly antisocial, very antisocial
		Strength/Degree	Assertiveness	NB	Very assertive, mildly assertive…		…mildly diffident
				NB	Very assertive, assertive, mildly assertive…		…diffident
			Assertiveness	B	Very assertive…		…mildly assertive, mildly diffident, diffident
				B	Assertive…		…mildly diffident, diffident
		Instrength/Indegree	Assertiveness	NB	Mildly diffident…		…assertive, mildly assertive
			Assertiveness	B	Mildly diffident…		…very assertive, assertive, mildly assertive
			Assertiveness	NB/B	Diffident…		…assertive
	Affiliative	Strength/Degree	Sociable	NB	Social…		…mildly social, mildly antisocial, very antisocial
Intra	Spatial	Strength	Sociable	NB	Social, mildly social, mildly antisocial…		…antisocial, very antisocial
	Agonistic	Strength/Degree	Assertiveness	NB	Very assertive…		…assertive, mildly diffident, diffident
				NB	Assertive…		…diffident
				NB	Mildly assertive…		…mildly diffident, diffident
		Instrength/Indegree	Assertiveness	NB	Mildly diffident, diffident…		…assertive, mildly assertive
				B	Mildly diffident, diffident…		…very assertive, assertive, mildly assertive
	Affiliative	*ns*					

Network: The spatial or interaction network for which metrics were calculated.
Scale: If 'Inter' the network only deals with intergroup links, if 'Intra' the network only deals with intragroup links.
Metric: Network metric for which significant difference is being tested (see definitions overview in section 6.2.1).
Attribute: Personality trait for which a significant difference in metrics is being tested.
Season: Study period (see section 3.2.1.1 for exact dates). NB = non-breeding season and B = breeding season.

In the non-breeding season intergroup spatial network, social and mildly antisocial takhi had greater betweenness, strength, and degree than mildly social, antisocial, and very antisocial takhi (Table 6.5). Members of CRG in particular had high metric scores, but social and mildly antisocial takhi from other groups did as well. Very assertive, diffident, and mildly diffident individuals tended to have greater degree than assertive takhi, indicating that CR and DB from CRG and juveniles from all three groups tended to be more often close to more members of other groups (Figure 6.4).

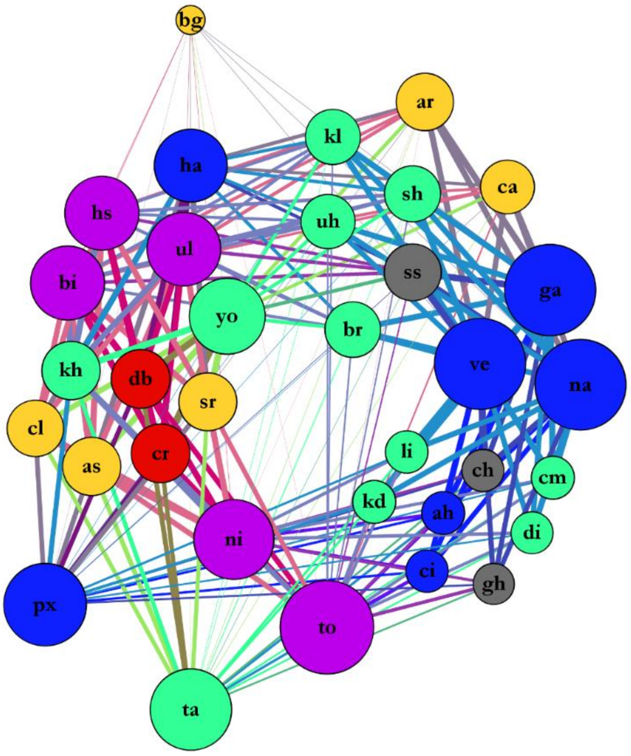


Figure 6.4. Sociogram showing the cross age Seer adult/juvenile intergroup spatial network for the non-breeding season. Node size represents network degree and colour represents assertiveness class; red= very assertive, yellow = assertive, teal = mildly assertive, blue = mildly diffident, purple = diffident, and grey = no score was calculated.

In the breeding season, social individuals were strongly connected in the intergroup agonistic network, as givers and receivers of interactions, even though they didn't have the highest strength or degree (Table 6.5). In both non-breeding and breeding seasons, more assertive individuals (adults) had higher strength and degree and less assertive individuals had higher instrength and indegree (juveniles). All individuals classified as social were strongly connected in the intergroup affiliative network.

All antisocial and very antisocial individuals in the non-breeding intragroup spatial networks had low strength scores, while individuals in the other categories showed much greater variation in strength score (Table 6.5). Trends in the non-breeding (and breeding for instrength/indegree) intragroup agonistic network appeared directly related to age, where more assertive individuals (adults) gave significantly more interactions and less assertive individuals (juveniles) received them.

6.3.4. Summary of results

The strongest and most consistent results observed in these analyses were the tendency for mares to manage intragroup cross age relationships, while stallions managed intergroup cross age relationships.

Stallions were the most central in intergroup agonistic interaction networks in non-breeding and breeding seasons. Stallions were most apt to give intergroup agonistic interactions, followed by non-lactating mares. Lactating mares gave significantly more agonistic interactions than colts, but not fillies. Non-lactating mares gave significantly more agonistic interactions than juveniles, and lactating mares gave significantly more agonistic interactions than colts. Juveniles received the most agonistic intergroup interactions. Stallions and colts engaged in intergroup affiliative interactions significantly more than other reproductive classes, but only during the non-breeding season. Affiliative interactions, and particularly play, occurred rarely overall, but were particularly uncommon intergroup during the breeding season (Table 6.2).

Mares, and particularly lactating mares, gave the most intragroup agonistic interactions, significantly more than stallions. In the breeding season, non-lactating mares gave significantly more intragroup agonistic interactions than stallions. Juveniles received significantly more agonistic interactions than adults. In the non-breeding season, non-lactating mares and stallions received more intragroup cross age agonistic interactions than lactating mares, and fillies received more than colts. BRG had very high intragroup affiliative interaction instrength in the non-breeding season because the filly TA, who soon after dispersed, engaged in mutual grooming with almost all the adult horses in the group.

Members of CRG continued to be central in intergroup spatial networks, although more so in the nonbreeding than in the breeding season. Intragroup trends at Seer and Hustai were challenging to interpret, as they appeared to be related to the ratio of adults to juveniles in each group, and influenced by group changes by individuals.

Social and mildly antisocial takhi tended to be central in intergroup spatial networks, a trend partly but not completely due to the centrality of CRG. Trends in centrality in agonistic networks relative to assertiveness were directly related to reproductive state. More assertive individuals (adults) tended to give inter- and intragroup interactions, and more diffident individuals (juveniles) tended to receive them.

Significant trends in network metrics relative to group membership and reproductive state at Hustai were not dependable due to the short time period of which Hustai data was collected. For more discussion see Chapter 7, section 7.3.4.

6.4. Discussion

The most important finding from this chapter was that mares tended to be more active in managing intragroup relationships, while stallions were most active in managing intergroup relationships. Colts and stallions engaged in significantly more cross age intergroup affiliative exchanges than any of the females, primarily play but also mutual grooming. Members of CRG were again significantly closer to other group members, but the trend was not as strong as was seen in adult and juvenile peer networks. Trends in centrality relative to personality were related to group membership and age, but intergroup spatial centrality relative to personality may have been partially independent of group membership.

6.4.1. The division of social responsibilities between mares and stallions

There was a clear division of labour in the agonistic interaction networks in both seasons at Seer. Stallions were significantly central as the givers of intergroup agonistic interactions to juveniles (Figure 6.5a, Figure 6.5b) and mares were significantly central as the givers of intragroup agonistic interactions (Figure 6.5c, Figure 6.5d). Adults gave all agonistic intergroup interactions and juveniles received them, except for only seven interactions out of a total of 317, six of which were given by fillies. Adults are dominant over juveniles (van Dierendonck et al. 1995, King et al. 2016) so it is expected that juveniles would be the recipients of most, if not all, cross age agonistic interactions.

The division in the giving of cross age agonistic interactions by sex among adults supports Rubenstein (1994)'s assertion that successful stallions limit the disruption of mares by extra-group individuals. The formation and maintenance of stable family groups in equid societies provides family stallions with more exclusive access to females and greater assurance of paternity (Feh 1990, Kaseda and Khalil 1996, King et al. 2016). For the assurance of paternity, they invest extra energy to ensure that the mares of their group are not harassed by other stallions, or disrupted by social and resource competition with non-family mares and juveniles, and overall have increased opportunities for resting and grazing (Rubenstein 1994, Linklater et al. 1999). If mares join stallions in part to minimise the need for them to engage in intergroup interactions, higher centrality of stallions in intergroup agonistic and affiliative networks is a logical result.

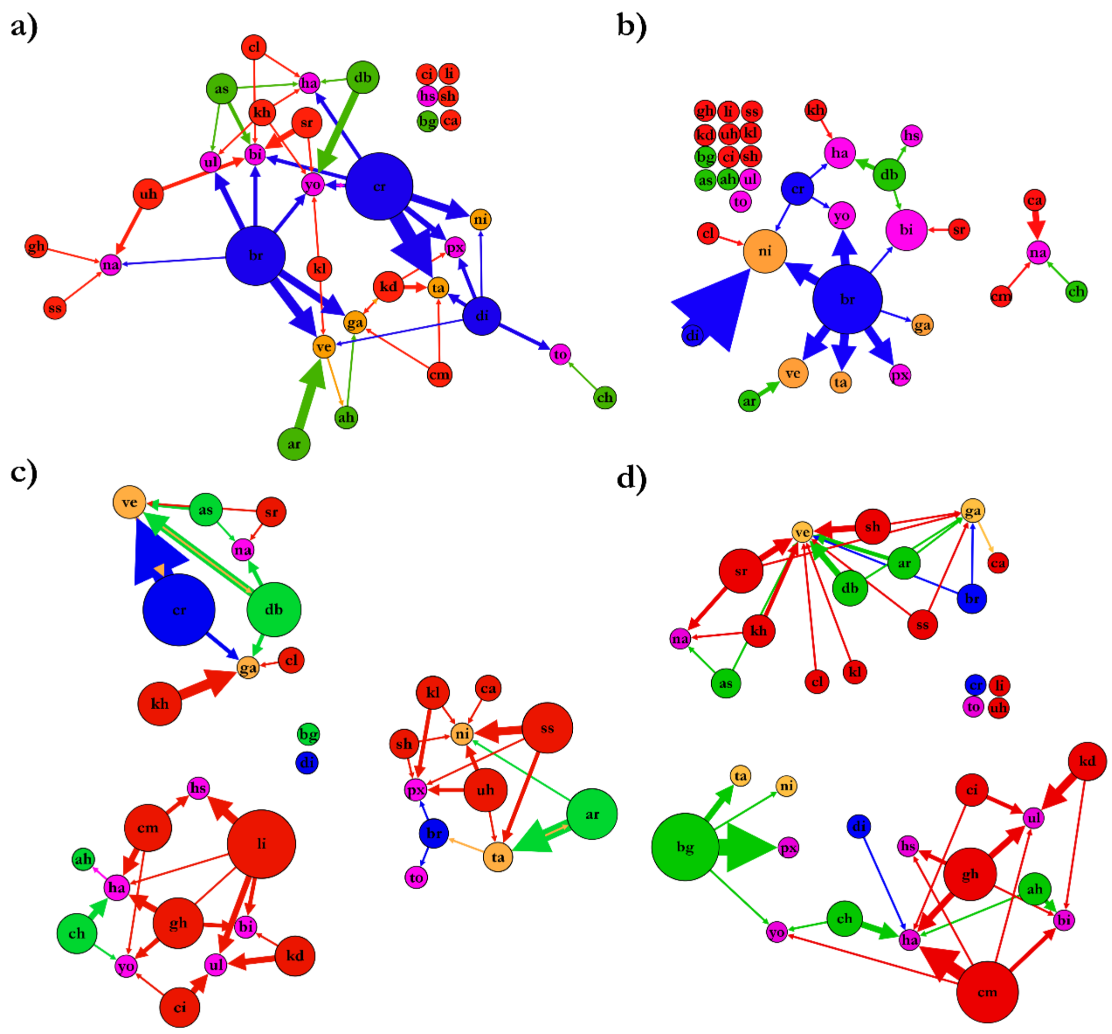


Figure 6.5. Sociograms showing the cross age Seer adult/juvenile (a) non-breeding intergroup, (b) breeding intergroup, (c) non-breeding intragroup, and (d) breeding intragroup agonistic networks. Node size represents network strength and colour represents reproductive state; blue = stallion, red = lactating mare, green = non-lactating mare, yellow = filly, and pink = colt.

Stallions will regularly leave family groups to inspect conspecifics from other groups (Berger 1986, Klimov 1988) or will travel and rest at the edge of the family group (Klingel 1975, Feist and McCullough 1976, King et al. 2016), so it was expected that they would also have greater spatial intergroup betweenness, strength, and degree than other reproductive classes. However, the interindividual distance measurements indicated that while stallions will sometimes move much closer to members of other groups than their own family, their median distance to members of other groups was no closer or further than other family members. This conclusion is supported by the results of Krueger et al. (2014), who found that all members of the family groups studied were equally likely to be located at the centre or the edge of their family group.

While stallions were active managing group borders, most within group space management was conducted by mares. Both lactating and non-lactating mares had significantly greater agonistic network strength and degree than juveniles in both the non-breeding and breeding seasons (Figure 6.5c, Figure 6.5d). The primary purpose of agonistic interactions is to maintain space between individuals (Feist and McCullough 1976, Feh 1988, King et al. 2016). Mild agonistic interactions such as head threats are not energetically costly and are usually offered when an unwanted receiver moves within ~1.5 m of the actor (Feist and McCullough 1976) and they are more often exchanged with between members of the same group (Table 6.2). Mares at Seer used mild threats (and sometimes more forceful interactions) to maintain personal space for themselves and their offspring while grazing or resting (Berger 1986, Rubenstein 1994), and thus had a more active role than stallions and juveniles in managing intragroup spatial relationships.

Mares directed most agonistic interactions towards juveniles other than their own offspring, and in no instance did a mare direct more interactions toward her own offspring than to others. More often her own offspring received fewer interactions than others in the group, but they did not generally receive more affiliative interactions in either the non-breeding or breeding seasons, as was reported by Stanley and Shultz (2012). Only two mother-offspring pairs were observed to engage in affiliative interactions; UL and CI in the non-breeding season, and CM and HS in the breeding season. Stanley and Shultz (2012)'s definition of an affiliative interaction included all occasions where one individual approached and made contact with another without also exchanging an aggressive interaction. A broader definition of affiliative interactions might result in a clearer bias towards offspring among dams at Seer and Hustai.

Fillies and colts had fairly equal agonistic interaction instrength and indegree across all seasons, within and between groups, and at both Seer and Hustai. Where significant differences in metrics between the two juvenile sexes occurred, fillies received a greater number of agonistic interactions and from more adults (Figures 6.6). In contrast, Stanley and Shultz's (2012) study found that colts received more aggression from adults of both sexes than did fillies. Colts had not been removed from the author's study site for a few years prior to the study period so that colts and potential bachelors were present, but during the study period some colts were removed from the group (Stanley and Shultz 2012). It is possible that human manipulation of the social groups, particularly the adding and removing of males of various ages, resulted in a more unsettled relationship between adults and non-offspring juveniles.

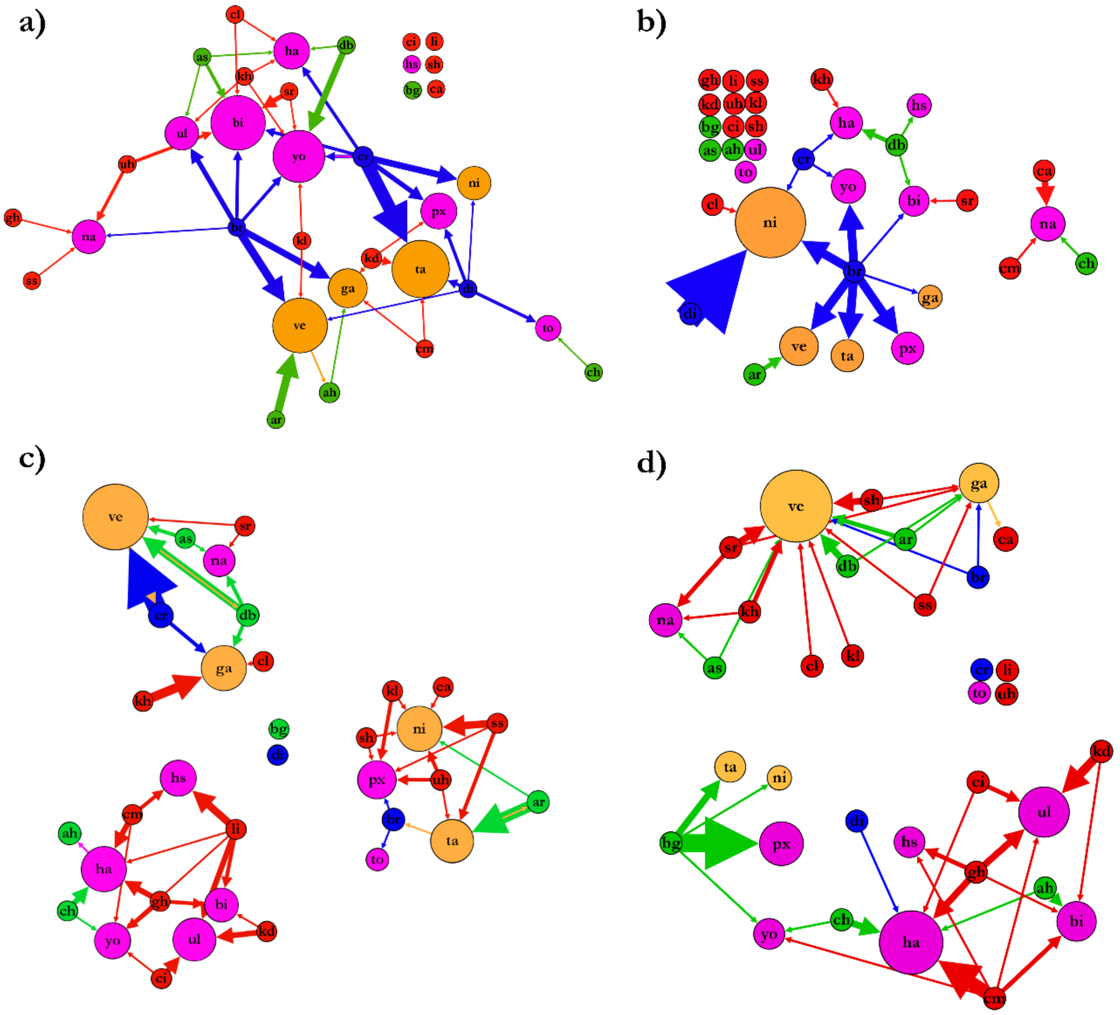


Figure 6.6. Sociograms showing the cross age Seer adult/juvenile (a) non-breeding intergroup, (b) breeding intergroup, (c) non-breeding intragroup, and (d) breeding intragroup agonistic networks. Node size represents network instrength and colour represents reproductive state; blue = stallion, red = lactating mare, green = non-lactating mare, yellow = filly, and pink = colt.

6.4.2. The role of non-lactating mares

After stallions, non-lactating mares were the next most active as the source of intergroup agonistic interactions (Figure 6.5a, Figure 6.5b). They were also the next most active after lactating mares as the initiators of intragroup agonistic interactions (Figure 6.5c, Figure 6.5d), especially in the breeding season. Non-lactating mares were expected to show a central role in agonistic interaction networks, and particularly in intergroup interaction networks, as during observations they appeared to be more active than lactating mares during intergroup encounters at both Seer and Hustai. They were observed to manage intergroup play interactions among juveniles and be involved during the visits of fillies with stallions from non-natal groups. In studies where mature stallions were not present, non-lactating and lactating mares were observed to devote more energy to intragroup and intergroup interactions (Rubenstein 1994, Sigurjónsdóttir et al. 2003), even displaying stallion-like behaviour (Berger 1999). Non-lactating mares, like stallions, have more energy resources available to devote to social 'policing' (Frank 1996) than pregnant or nursing mares, and at both Seer and Hustai appeared to occupy dominant positions within their groups. This supposition was supported by the centrality of non-lactating mares in both intra- and intergroup agonistic networks. They were also the only adult mares connected in intergroup affiliative networks (Figure 6.7).

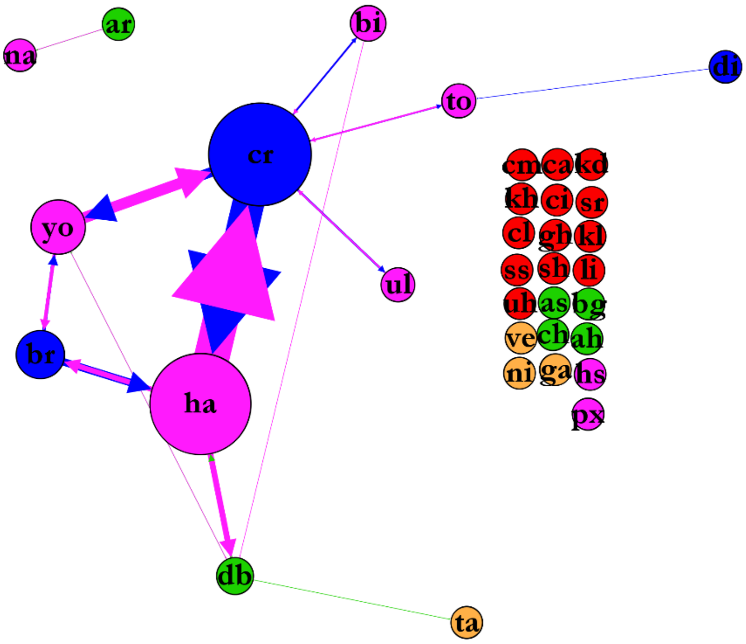


Figure 6.7. Sociogram showing the cross age Seer adult/juvenile intergroup affiliative network for the non-breeding season. Node size represents network strength and colour represents reproductive state; blue = stallion, red = lactating mare, green = non-lactating mare, yellow = filly, and pink = colt.

6.4.3. Pre-dispersal affiliative ties

Colts and stallions were significantly central in intergroup affiliative networks during the non-breeding season (Figure 6.7), and most of the interactions were play, rather than mutual grooming (Table 6.2). One of the non-lactating mares (DB) and one filly (TA) also engaged in intergroup play, but not as much or as frequently. The breeding season intergroup affiliative network was too sparse for analysis (27 interactions but only involving three pairs of horses) but only involved colts and family stallions. The importance of play to juvenile development has been discussed in Chapter 5, section 5.4.6. Play between colts and family stallions is a continuation and extension of this development. Play with other family stallions allows colts to learn and develop skills from males already known to be socially effective. Because play is a low risk method for deciding questions of dominance (Goodwin and Hughes 2005) play between colts and stallions may reduce the frequency and severity of more agonistic encounters post-dispersal. Berger and Cunningham (1987) found that family stallions acted aggressively towards unfamiliar bachelors, but played with those with whom they were familiar. At Seer, stallions showed varying responses to post-dispersal colts who had been previous playmates. One colt (TO), post-dispersal and travelling alone, was allowed to travel and graze close to the family groups for over an hour during data collection. Another colt (YO) who was very active in intergroup play pre-dispersal, left the family groups in spring and, along with several other dispersing juveniles, joined an older maverick mare (BG). For the rest of the summer observation period, YO was driven off if he came too close to the family groups. The presence of females (BG and the post-dispersal fillies) may have changed the reaction of the family stallions towards their post-dispersal playmates, regardless of previous familiarity. At both Seer and Hustai, family stallions were only very rarely observed to play with stallions from other families. On one occasion, two family stallions were observed to participate in an intergroup play session, but when one of the family mares followed her yearling son over and began threatening the stallion of the other family, the stallion of the mare's group immediately stopped playing and deliberately separated the families (Figure 6.8).

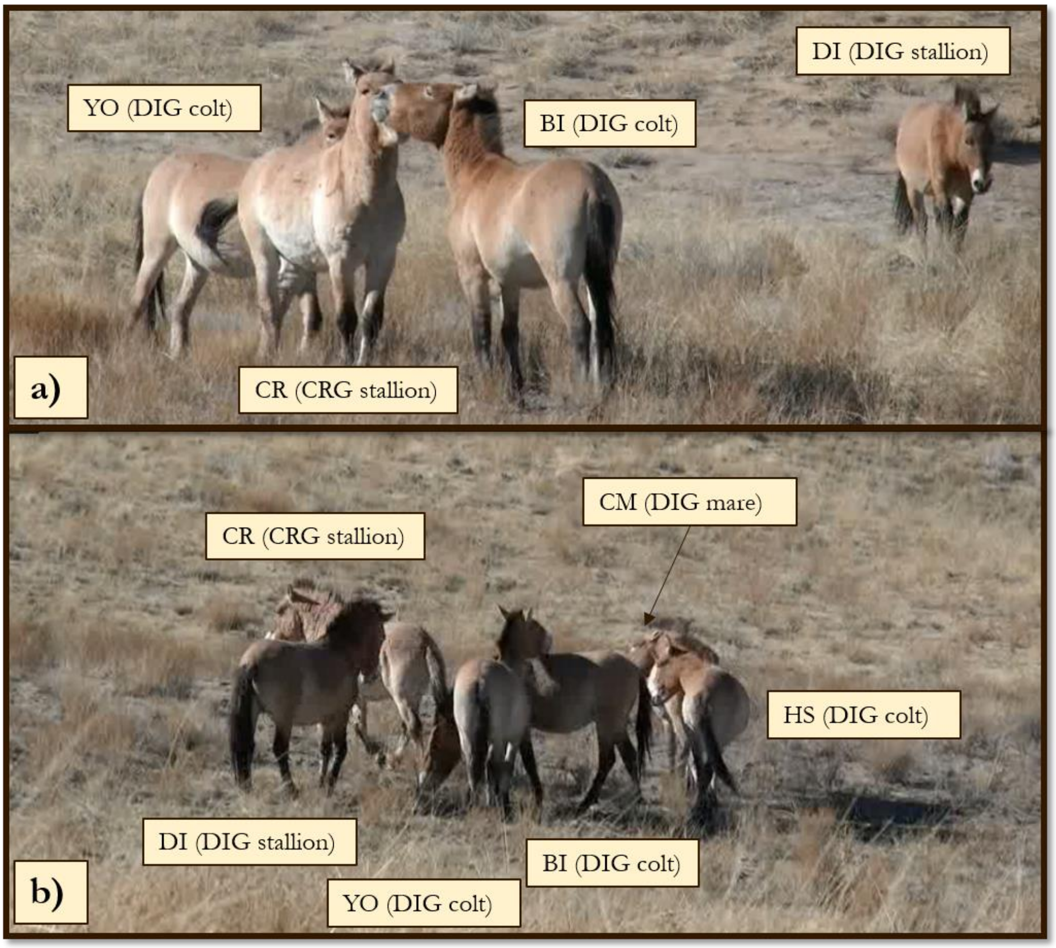


Figure 6.8. Video stills from Seer non-breeding season observations showing the change in posture of family stallions during an intergroup play session (a) before and (b) after the arrival of a family mare. The mare (CM) is the dam of HS and BI, and followed her younger son (HS) over to the play session. Although partly hidden, she is shown giving a head threat to CR.

Overall, intergroup play potentially benefits both stallions and colts by developing the physical and social abilities of colts, providing opportunities for stallions to practise skills while enforcing their dominance, and by allowing all individuals to learn about the abilities of potential future competitors (Berger 1986, Feh 1988, Kaseda and Khalil 1996, Cameron et al. 2008).

The occurrence of intergroup mutual grooming at Seer appeared to be promoted by the herd structure of the three main family groups. All intergroup mutual grooming occurring during observations involved colts: YO, TO, and UL all mutual groomed with CR, HA with BR, and NA with AR. Once, outside of the observation period a post-dispersal TA (a filly) mutual groomed with AH, a non-lactating mare. Mutual grooming is only observed between individuals who are familiar with each other (King et al. 2016), and in previous studies usually only occurred between members of the same social group (Feist and McCullough 1976, Wells and Goldschmidt-Rothschild 1979, Sigurjónsdóttir et al. 2003, King et al. 2016). Tyler et al. (1972) observed intergroup mutual grooming between a mother and her post-dispersal daughter. Bachelors will also engage in mutual grooming (Christensen et al. 2002). It is probable that the herd structure at Seer increased the familiarity of juveniles with non-family members to the point that they were comfortable mutual grooming with them. Using co-group membership as a metric for familiarity, as was done in Chapter 4, therefore may not represent an accurate measure of familiarity in situations were multiple family groups form a herd. However, as of December 2017, none of the fillies who dispersed during the study settled in the groups of either their fathers or of colts from their natal group (Association pour le cheval de Przewalski: TAKH 2017b). Taken together, mutual grooming between the members of other groups and the post-dispersal group membership of juveniles suggest a potential need for a more nuanced definition of familiarity than simple co-family membership.

6.4.4. Reduced centrality of CRG

Members of CRG were not as strongly central in intergroup spatial networks when only ties between adults and juveniles were considered. CRG members were more central than members of DIG, but only in the non-breeding season (Figure 6.9a). During the breeding season the fillies GA and VE, who had very high strength, changed groups to BRG. Their already high centrality as members of CRG was increased by having intergroup ties to both BRG and CRG (Figure 6.9b). However, overall adults and juveniles of CRG remained significantly closer to the juveniles and adults of BRG and DIG than were the members of BRG and DIG to each other. Potential reasons for the significant centrality of CRG were discussed in Chapter 4, section 4.4.1 and Chapter 5, section 5.4.1.

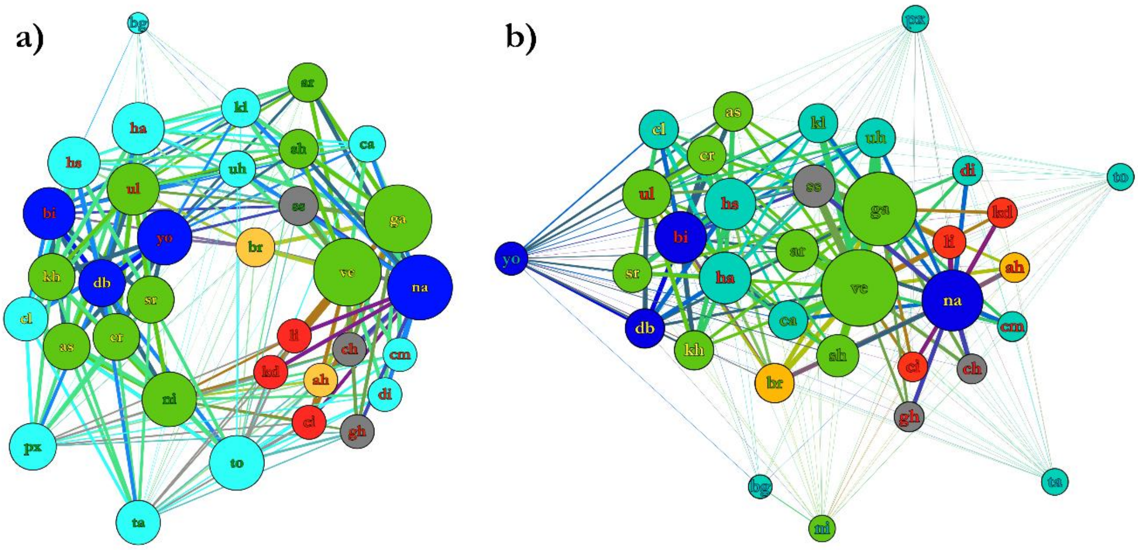


Figure 6.9. Sociogram showing the cross age Seer adult/juvenile intergroup spatial network for the (a) non-breeding and (b) breeding seasons. Node size represents network strength and colour represents sociability class; blue = social, sky blue = mildly social, green = mildly antisocial, yellow = antisocial, red = very antisocial, grey = no score was calculated.

6.4.5. Personality trends

Significant relationships between spatial centrality and personality followed those observed in Chapters 4 and 5, with social and mildly antisocial individuals tending to be more central. The centrality of social and antisocial takhi was related to the centrality of CRG, and the strength of this relationship was supported by the fact that significant trends in centrality relative to group membership and personality were both only detected during the non-breeding season. However, visual inspection of the network again shows that the social and mildly antisocial members of BRG and DIG also had higher strength and degree and a more central position in the intergroup spatial network during the non-breeding season (Figure 6.9a). As was discussed in Chapter 5, section 5.4.4, further research should investigate whether the tendency for mildly social individuals to be more peripheral, and for social and mildly antisocial individuals to be more central in intergroup spatial networks proves to be a consistent result across time or can be found in other takhi populations.

6.4.6. Hustai trends

Hustai datasets were again too sparse to draw strong conclusions about the centrality of some individuals in agonistic and affiliative interaction networks. Spatial trends relative to reproductive state were based on a slightly larger dataset, but still limited in the number of overall days of observation (see Chapter 3, section 3.2.1.1 for exact dates). In the non-breeding season, lactating mares and juveniles were significantly more central than non-lactating mares and stallions. The lack of significant centrality may have only been observed during the non-breeding season because many of the older juveniles, particularly from BDG, had dispersed by the breeding season. Consistent with the trends observed at Seer, in both the non-breeding and breeding season, fillies (colts as well in the non-breeding season) received significantly more intragroup agonistic interactions than adults. For further discussion of the limitations of the Hustai data, see Chapter 7, section 7.3.4.

6.5. Chapter Outcomes

The purpose of this chapter was to assess whether adult/juvenile relationships in intragroup and intergroup spatial, agonistic, and affiliative networks were influenced by the group membership, reproductive state, or personality of individual takhi.

Main chapter findings were as follows:

- Mares, and particularly lactating mares, managed the intragroup distribution of juveniles, and stallions managed the intergroup distribution of juveniles. Mares were the most active as the givers of interactions in intragroup agonistic networks, and stallions were the most active in intergroup agonistic networks.
- Juveniles of both sexes received nearly all the agonistic interactions exchanged between age-classes, both within and between groups.
- Non-lactating mares, but not lactating mares, also often gave intergroup agonistic interactions, although not as frequently as stallions.
- Colts and stallions engaged significantly more in cross age class intergroup affiliative interactions than did female takhi.
- Members of CRG were significantly more central to the Seer intergroup spatial network, as was observed in peer adult and peer juvenile networks, but only in the non-breeding season.
- Mildly social individuals tended to be peripheral in intergroup spatial networks. The trend was related to the centrality of the social and mildly antisocial members of CRG, but not completely explained by it.
- At Hustai matrilineal subfamilies, made up of lactating mares, colts, and fillies, tended to have higher intragroup spatial centrality than stallions or non-lactating mares.

The next chapter (Chapter 7) will bring together the results of Chapters 2, 4, 5, and 6, discuss the resulting broader picture of takhi social structure, and explore how the results can be applied to future takhi management and conservation efforts.

7. Discussion

7.1. Review of research aim and objectives

The overall aim of this study was to investigate potential behavioural mechanisms of social cohesion in reintroduced takhi, exploring mechanisms of social cohesion both within and between family groups to better understand observed variation in cohesion at the group and herd level in reintroduced takhi populations. A better understanding of factors influencing cohesion will aid in the development of adaptive management strategies and the mitigation of known threats to the persistence of takhi in Mongolia. This thesis focused on individual variation as a potential source of observed variation in social cohesion. The spatial distribution of individuals was used as a surrogate measure of cohesion, and potential mechanisms included the social interactions between individuals and variations in the characteristics of the individuals themselves. Individual characteristics investigated included group membership, reproductive state, and personality type.

7.2. Main findings

Initial management efforts at all three reintroduction sites in Mongolia were focused on ensuring takhi had sufficient access to food and water and were provided with room to roam with reduced competition from domestic livestock (van Dierendonck and Wallis de Vries 1996, Joly et al. 2012, Burnik Sturm et al. 2017). Establishing reserve areas where the presence of livestock was kept to a minimum, some enclosed by fence and some not, and with varying levels of legal protection, ensured initial availability of sufficient space and resources (van Dierendonck and Wallis de Vries 1996, Association pour le cheval de Przewalski: TAKH 2013). While this management strategy was effective for the initial establishment of the reintroduced populations, it is only practically applicable within restricted areas such as the release sites. If the reintroduction projects are successful in developing multiple sub-populations large enough to persist without need of further supplementation of individuals, the number of takhi present will be much greater than the carrying capacity of the current reintroduction sites (van Dierendonck and Wallis de Vries 1996, Kaczensky et al. 2016, Association pour le cheval de Przewalski: TAKH 2017a). Once groups of takhi move outside of established reintroduction sites, contact and competition with livestock, including domestic horses, will be inevitable. Takhi managers will need to develop management strategies that ensure the persistence of takhi populations even when takhi and livestock share the same rangeland. Management strategies informed by an understanding of takhi social structure and what behaviours and individuals keep groups together or drive them apart will help managers reduce risk of conflict and competition with livestock and hybridisation with domestic horses.

Identifying which individuals play important roles in maintaining intra- and intergroup cohesion, and how they influence cohesion can allow targeted management of growing takhi populations. For example, some stallions at both Seer and Hustai appeared to be significantly more tolerant of closer intergroup proximity. From a management perspective, these stallions and their families could serve as social glue connecting multiple families in a broader social network. However, their tolerance of conspecific proximity could include tolerance of domestic horse herds, making those families potential disease vectors or sources of takhi-domestic horse hybrids.

7.2.1. Overview of main findings

Overall, reproductive state mostly clearly dictated individual influence on intra- and intergroup cohesion, but group membership influenced intergroup cohesion and personality appeared to have some effect as well.

The main findings from analyses, in order of the research chapters in which they were presented, were as follows:

Chapter 2 - Repeatable personality traits could be assessed using field-based methods. Aside from intergroup spatial networks, personality did not have a clear and consistent effect on intra- or intergroup cohesion. Other trends in intra- and intergroup cohesion relative to personality were obscured by correlations between personality and reproductive state.

Chapter 4 - Stallions gave more intergroup agonistic interactions than mares, particularly in the non-breeding season. Members of CRG occupied a spatial broker position between the other family groups, and mildly social individuals tended to be peripheral in intergroup spatial networks.

Chapter 5 - Colts were more involved in intergroup affiliative interactions than fillies. Within groups, fillies more often groomed and colts more often played. As with adults, members of CRG occupied a spatial broker position, and mildly social individuals were more peripheral in intergroup spatial networks.

Chapter 6 - Mares gave most intragroup agonistic interactions, and stallions gave most intergroup agonistic interactions. Males of all ages were much more active in intergroup affiliative networks than females. The broker position of CRG was less strong in adult/juvenile networks.

7.2.2. Developing methodology for assessing takhi personality in Chapter 2

This study is one of the first to apply non-invasive methods of assessing personality in free-living equid populations (see also Baker 2015) and may be the first to use observer ratings as a method of producing repeatable personality scores for takhi. Briard et al. (2015) used observer ratings to assess the personality trait ‘boldness’ in a herd of domestic mares. Berger (1977) used ethological coding to develop an ‘index of nervousness’ for individuals in families of feral horses based on their vigilance while drinking. No other studies were found in the literature which assessed personality traits in groups of free-living equids.

In this study, both ethological coding and observer rating methods produced significantly repeatable personality trait scores. Observer rating methods yielded two traits, sociability and assertiveness, which were repeatable across multiple observers, while ethological coding yielded one personality trait, sociability, with scores repeatable across multiple seasons. The significant correlation between sociability scores produced by observer rating and by ethological coding lends confidence to the results of both methods. Either ethological coding or observer rating or both appear to be dependable methods for assessing takhi personality, but both require data collected across an extended time period (based on this study, >8 hours of observation across multiple time periods). Time is necessary for ethological coding to have a high enough frequency of interaction occurrences for analysis. Time is necessary for observer rating to allow the observers opportunity to develop impressions of individual takhi across varied environmental and social situations.

From observer rating it was possible to describe two independent personality traits, while ethological coding could only capture one. Baker (2015) extracted eight independent personality components (essentially traits) from ethological coding data, of which the two components accounting for the most variation in the data described sociability and assertiveness traits. Future research at Seer and Hustai should investigate whether larger ethological coding datasets could use factor analysis rather than interaction categorization (Chapter 2, section 2.2.2.3) and then also detect assertiveness as a personality trait independent from sociability. Extracting sociability and assertiveness traits independently using both observer rating and ethological coding methods would offer strong support that both are personality traits consistently expressed by takhi.

Even if an increase in takhi population size reduces ranger familiarity with individual takhi, multiple observers collecting ethological coding data on the same animals would have sufficient time during data collection to develop an impression of each focal individual’s personality, and could rate focal individuals at the conclusion of data collection, as was done by Briard et al. (2015). Thus, even as takhi populations grow, observer rating and ethological coding methods could be used together to compare and verify assessments of takhi personality, which could then be incorporated into other analyses (Gosling and Vazire 2002, Highfill et al. 2010, Watters and Powell 2012).

Sociability and assertiveness traits were assigned to all individuals older than six months at Seer. Both rating and coding methods for foals younger than six months did not show repeatable results. This was probably because there was a shorter time period available for personality assessment of young foals and the rapid development in the social behaviour of foals during the first six months resulted in biased personality assessments of foals of staggered ages (see Chapter 2, section 2.4.2). In future, effective assessment of foal personality would require periods of intense monitoring during each stage of the foal's social development (Boyd 1988a), and further research into how observed personality is expressed during different stages of development in the first six months of life.

7.2.3. Summary and synthesis of SNA results from Chapters 4, 5, and 6

Social network analysis of the social structure at Seer showed that stallions were central in all agonistic interaction networks in which they were involved, stallions and colts were centrally active in intergroup affiliative networks, and mares gave the majority of within group agonistic interactions directed at juveniles. CRG was spatially central in the Seer herd, and mildly social takhi of all ages tended to be spatially peripheral.

7.2.3.1. Stallions as intergroup border managers

Stallions had greater intergroup agonistic strength and degree than other takhi in adult peer and adult/juvenile networks in both non-breeding and breeding seasons. In the non-breeding season, where more interactions occurred generally (see section 7.3.3), stallions also had greater betweenness than all other takhi. Thus, although stallions were not, on average, significantly more spatially peripheral in family groups than were other group members, they were active managers of the group borders and used agonistic interactions to maintain group boundaries. If stallions are the most active reproductive class in managing group borders, then relationships between stallions, and an individual stallion's tolerance for the close proximity of extra-group members, may be an important predictor of intergroup cohesion. The spatial centrality of CRG suggests that this is the case at Seer. The DNG family group at Hustai was almost always found in close proximity to bachelors or other family groups. During one observation period, the family spent the better part of two hours resting <100 m from a group of five bachelors, and the family stallion grazed and rested closer to the bachelors than to his family without exchanging any agonistic interactions. In contrast, the stallion of the KEG focal group drove his family almost one kilometre after a brief confrontation with a lone bachelor. As the past relationships of both Hustai stallions to their respective bachelors was unknown, it is impossible to say whether past familiarity or other factors may have contributed to the reactions of both stallions, but the effect of the different reactions on their ultimate intergroup spacing is worth note.

In previous studies, while most of the intergroup interactions observed occurred between family stallions or between stallions and bachelors (Berger 1977, Feist and McCullough 1976, Duncan and Vigne 1979, Rubenstein 1981, Rutberg 1990), the longer-term relationships between stallions were not reported. Further research should investigate how interstallion relationships change over time, and whether changing relationships between family stallions are accompanied by changes in intergroup spacing. If consistent trends are observed, it might be possible to predict herd level changes in cohesion from observed changes in interstallion relationships. Predicted changes could then be included during the planning and development of adaptive management schemes aimed at promoting strong spatial and social cohesion in growing takhi populations (see section 7.4.1. for further discussion).

7.2.3.2. Building long-term intermale relationships

Colts and stallions were both more central than females in intergroup affiliative networks as both givers and receivers of interactions. Most affiliative interactions between colts and stallions were play and most occurred during the non-breeding season. Play between colts and between colts and stallions builds relationships between males who will be future competitors (Berger 1986, Feh 1988, Kaseda and Khalil 1996, Cameron et al. 2008) or potentially future allies (Feh 1999). Intergroup affiliative exchanges between males as they mature may promote intergroup stability and cohesion as adults. In most captive and semi-feral situations, individuals, usually males, are often added and removed from the population in the interest of promoting certain bloodlines (Tyler 1972, Boyd 1991, Stanley and Shultz 2012). These active management practices result in a social structure very different from what would occur naturally, with stable family groups and stallions with sometimes over a decade of tenure in their group (Berger 1986, Rubenstein 1994). Tilson et al. (1988) had mixed success in their efforts to artificially create takhi stallion bachelor groups with colts and stallions of varying ages and from four different locations who had not had a previous social history. The higher reception of aggressive interactions by colts than fillies observed by Stanley and Shultz (2012) may have been the result of unsettled social relations due to the adding and removal of colts and stallions before and during the study. Long-term relationships between stallions may have a more important role in maintaining stable intergroup social structure than has previously been acknowledged. The colts at Seer began to build social relationships with other males at a young age. Further research should investigate how juvenile relationships with peers and adults shape later intermale relationships, the behaviour of those stallions who go on to form family groups, and herd level social structure. The relationships of colts and stallions over time may be a key part of how cohesive herds are formed.

7.2.3.3. Mares managing intragroup social structure

In peer relationship networks, both adult and juvenile, neither reproductive state nor personality had a significant influence on intragroup interaction centrality. However, mares were significantly more central as the givers of agonistic interactions to juveniles in both seasons. Thus, while stallions managed group borders, mares were active managing the spatial distribution of juveniles within the group. Intragroup spatial management by mares probably arose from personal space maintenance and protection of younger offspring.

Mares need time and space to graze (Rubenstein 1994) and use agonistic interactions to prevent juveniles and stallions from interfering. Lactating females with foals at heel have the greatest need of constant access to both grazing and water sources (Boyd 1991, Rubenstein 1994, Nowzari et al. 2013, Schoenecker et al. 2016). Mare also use agonistic interactions to protect their foals (particularly new foals) from accidental or deliberate injury from other group members (Boyd 1988a, Stanley and Shultz 2012). Mortality rates are higher in foals than in pre-senescence adults (Ransom et al. 2016) and highest in foals immediately following birth (Berger 1986, Feh 2005). Finally, if stallions primarily invest their energy in maintaining group borders, but not in controlling within group spatial distribution, except in reference to the presence and position of other groups (Wells and Goldschmidt-Rothschild 1979, Krueger et al. 2014), that would leave mares at the centre of intragroup agonistic interaction networks. All the above are potential drivers of the centrality of mares in intragroup agonistic networks.

The results of this study did not identify any factors beyond co-group familiarity which may have contributed to intragroup or intergroup proximity maintenance in adult mares. Future research should investigate new ways of measuring socially attractive forces between mares, both within groups and between groups (see sections 7.3.3 and 7.5.5 for more discussion). Mares kept juveniles and peers at predefined distances within the group, but it was unclear how cohesion among mares was promoted. Van Dierendonck et al. (2004) proposed that intermare relationships are formed through proximity and mutual grooming. Mutual grooming occurred only rarely between adult peers at Seer, and so did not appear to be an important part of relationship maintenance. Finer scale analysis of spatial data, dealing with hourly or quarter-hourly changes in spatial distribution could potentially identify preferred neighbours among mares within family groups. Further research should explore how mare peer relationships are maintained, particularly whether and how connections are maintained with peers in other groups and how familiar the members of other groups are perceived to be. During observations at Seer, the mare CA was observed whinnying to members of the other family groups when they moved out of sight or were moving back within range, which indicated she perceived them as part of her social group, although not members of her family group. Nuances of perceived familiarity may be the primary mechanism promoting variation in intergroup cohesion in takhi, and future research should investigate methods of assessing varying degrees of familiarity and determine how this variation contributes to cohesive behaviour in takhi.

7.2.3.4. CRG as a spatial broker

Members of CRG occupied a spatial broker position in the herd at Seer. This may be because of the seniority and stability of the group (Rutberg 1990), and may be because of the highly social behaviour of some of the group members (Chapter 4, section 4.4.1). CRG's intergroup centrality was stronger in adult peer networks than in the juvenile peer and adult/juvenile intergroup spatial networks. The dispersal of two of the three CRG juveniles reduced the centrality of CRG in networks that included juveniles.

The intergroup proximity tolerance and cohesion promotion of CRG was also observed in the DNG group at Hustai. It may be that members of both DNG and CRG were more tolerant of close proximity to other groups. The stallion of CRG, CR, was more frequently observed to engage in affiliative intergroup interactions than the other family stallions, and one of the CRG mares, DB, was the only adult mare observed to engage in affiliative intergroup interactions. Both CR and DB also had the highest assertiveness scores of the Seer population (Chapter 2, Figure 2.2b). Thus, it may be that high social activity of these two (or other) individuals in CRG contributed to the observed centrality of CRG as a group. It may also be that CR's tolerance of close proximity to other family groups was a major factor contributing to CRG occupying a spatial broker position between BRG and DIG.

7.2.3.5. The influence of personality on intergroup cohesion

Although other studies have reported a difference in intragroup spatial position relative to personality in free-living equids (Berger 1977, Baker 2015, Briard et al. 2015), to date no other study has looked at the influence of personality on intergroup spatial positioning. The centrality of social and mildly antisocial takhi in both peer and the adult/juvenile networks appeared to be related to the centrality of CRG, but social and mildly antisocial takhi from the other groups tended to be more central as well. Thus, the personality composition of CRG may have contributed to its intergroup centrality. Further research is necessary to confirm the role of personality in the centrality of CRG. If mildly social individuals are consistently more peripheral in intergroup networks, sociability could potentially be used to predict the cohesive tendencies of individuals and their potential influence on intergroup social structure.

7.3. Study limitations

7.3.1. Ongoing development in SNA

Development of methods for analysing animal social networks has been ongoing while this study was underway. Two methods of SNA receiving more attention recently and which could be applied to the data collected for this study, are dynamic network analysis and the use of pre-network permutations for the creation of null models.

7.3.1.1. Dynamic networks

Animal SNA researchers have increasingly begun advocating the application of dynamic network analysis, rather than aggregating data from an extended time period to create one static network intended to describe the study population (Blonder et al. 2012, Farine and Whitehead 2015, Rubenstein et al. 2015). Dynamic network analysis requires more data than static network analysis, as the network of each time stamp must be sufficiently dense (Farine and Whitehead 2015). Rubenstein et al. (2015) used dynamic network analysis to demonstrate previously undetected differences between Grevy's zebra and onager social structure. Based on static network analysis, both species were observed to display the same fission-fusion social structure (Sundaresan et al. 2007), but when examined using dynamic network analysis, Grevy's zebra were found to move from one herd to another in subgroups of more than one individual, while onagers would move from herd to herd alone or in pairs (Rubenstein et al. 2015).

The analyses applied in this study could be considered semi-dynamic, in that both spatial and interaction networks were broken down into separate networks for each season of observation, thus capturing variations in structure with the progression of time. However, only two study periods were used and each one covered an extended period of time. Interaction networks broken down below the season level (daily, weekly, or fortnightly networks), particularly at Hustai but also at Seer, would be too sparse for any dynamic analyses. The spatial data, however, would be a prime candidate for the application of dynamic network analyses, as multiple measures of interindividual distance are available for each dyad for each week, and even day, of observation. The application of dynamic network analysis to the spatial network datasets developed in this study is beyond the scope of this thesis, but would be an interesting next step for analysis.

7.3.1.2. Pre-network permutations

The node permutation method applied to the interaction datasets made relatively large changes to the observed network to create the random networks. Previous studies have found that node permutation methods sometimes created random networks that would never actually be seen in the observed study population, leading to elevated type I and type II error rates (Farine and Whitehead 2015).

Weight permutations, unlike node permutations, maintain network topology (Opsahl et al. 2008). While in this study weight permutation methods were effective for randomising the spatial networks, which were fully connected, they could not be used for the sparser interaction networks. Often an interaction only occurred once between a pair of takhi. As a result, there was often limited variation in the weight of links in the interaction networks. Weight permutations redistributed weights in networks but never added links where they did not occur before. Thus, the randomised versions of interaction networks using weight permutations would have been very similar to the observed network and no significant difference between the observed and random networks could be detected. Overall, in this study weight permutations methods were too restrictive to be used to detect significant differences between classes in sparser interaction networks, while the node permutation method used held the risk of not being restrictive enough.

In a recent paper, Farine (2017) advocated the application of 'pre-network' data permutation as a way to create random networks while maintaining basic network structure and reducing type I and type II error rates. Pre-network permutation essentially permutes the data prior to calculating the edge weights for the observed network (Farine 2017). For example, the fall spatial network for Seer was created by calculating the median of the median-per-hour interindividual distances of all present pairs of takhi (Chapter 3, section 3.2.3.1.3). Pre-network permutations of those data would entail swapping median-per-hour, or even per interval, measurements between pairs of takhi. So, if during the first hour of observation on October 15th, CM and HS were 15 m apart and AR and BR were 30 m apart, the pre-network shuffle might swap those measurements, so that CM and HS were now 30 metres apart and AR and BR were 15 m apart. This change would slightly increase the median of the median-per-hour distance between CM and HS, but would not cause as great a change in the final network structure as if the median of the median-per-hour scores between CM and HS and AR and BR were swapped in the final network. Farine (2017) describes a method for permuting focal observation data which could be particularly applicable to the interaction networks used in this study. In focal observation pre-network permutations, one individual from each focal observation is chosen (for example SS during observation #60) and one interaction with another individual (perhaps a head threat to UH) is swapped with that of an individual from another focal observation (perhaps BR during observation #14 giving a head threat to VE). In the newly permutated dataset, during observation #60 SS gives a head threat to VE and during observation #14 BR gives a head threat to UH. Multiple swaps are repeated through the observed data, and then a randomised null model interaction network for the season is calculated. In the random network, the rate of head threats from SS to UH is a little lower than in the observed network, while the rate of head threats from SS to VE is higher than in the observed network.

This study applied network permutation methods to static networks created from aggregations of temporally dynamic data. Methods of SNA are being developed that can be applied to temporally dynamic networks (Farine and Whitehead 2015, Rubenstein et al. 2015) and that permute network input data in a way that maintains basic data structure and topology while minimizing type I and type II error in test results (Farine 2017). Future research into takhi social structure could use the same data sets and data collection methods presented here but apply the more progressive analysis methods of dynamic network analysis and pre-network permutation.

7.3.2. Ranger consistency

Interaction networks at Seer and Hustai were sometimes quite sparse, depending on interaction type and season (see Chapter 3, Table 3.6). Sparse datasets require greater confidence in the accuracy and precision of observations, although, perhaps with the exception of controlled in-lab experiments, interaction datasets are almost always incomplete (Croft et al. 2008). As was discussed in Chapter 3, section 3.2.1.3.1, interaction observer agreement for the Seer data varied a great deal and observer consistency for the Hustai data were not tested due to time constraints. Because the takhi at both locations were not observed 24 hours a day, even with 100% agreement between rangers during the period of observation, the observed networks would still represent a model of the true interaction networks, not the true networks themselves.

The occurrence of overt interactions between free-living equids is relatively rare (King et al. 2016). Studies exploring equid SNA often found interactions occurred too infrequently to be able to develop an adequate dataset for analysis (Briard et al. 2015, Stanley et al. 2018). When equid social encounters do occur, interactions can occur very quickly over a short period, which increases the chance observers missing some interactions.

Observer agreement at Seer and Hustai was further complicated by differences in language, as observers spoke English, French, and Mongolian as a first language. Even when observers are equally fluent in the same language, cultural background can influence each observer's perception and/or prioritization of behaviour (Zukosky 2016), so that even a direct translation of a behaviour definition will not necessarily result in complete observer agreement. For example, Zukosky (2016) described how biologists at the Kalamaili takhi reintroduction project in China developed an ethogram where the response of individual takhi to an agonistic interaction was considered the central subject of the interaction, while in ethograms from more 'western' cultures, such as Europe or the US, individuals giving agonistic interactions are usually considered the central subject and the response of the receiving individual, although often recorded, considered secondary. The nuance of perception of the point where an interaction transitions from being a head threat, to a charge, to a chase, is challenging to collectively define and establish between observers with similar cultural backgrounds speaking the same language, and was even more challenging for this study.

To increase interaction observer agreement in future analyses, ideally multiple observer training sessions would be held, with a fluent translator of each represented language present also familiar with equid interaction types. Training sessions would include a combination of sessions using a series of video clips showing multiple examples of each interaction of interest and sessions together in the field observing and discussing interactions as they occurred. Once data collection began, regular simultaneous observations (monthly, fortnightly, or even weekly) would be conducted, during which all trained observers independently observed and recorded interactions from the same focal group at the same time. These observations could be used to monitor observer agreement levels, and target areas where training methods required adjustment or further discussion. Of course, the scenario described above represents an absolute best-case scenario for data collection, which is a luxury rarely available for most studies.

7.3.3. The seasonality of interactions

More interactions occurred in the non-breeding season than in the breeding season at Seer. In adult peer networks the ratio of non-breeding to breeding agonistic interactions was 1.7:1. The ratio of affiliative interactions was 1:1 but adult affiliative interactions were very sparse overall. In adult/juvenile networks the ratio of non-breeding to breeding agonistic interactions was 1.5:1, and for affiliative interactions was 6.6:1. Takhi were less active during the day in summer, often resting close together over sand or rock, or under shelter to avoid flies. Bouts of play were less frequent and more apt to occur between co-group members than between members of different groups (Chapter 6, Table 6.2). If individuals, usually colts, were not visiting other families for play sessions, they were also less likely to be involved in agonistic intergroup interactions. By the end of the first month of the breeding season, eight of the twelve juveniles present in the non-breeding season in the Seer family groups dispersed, and so were no longer engaging in the affiliative herd intergroup interactions. All these factors may have contributed to the reduced frequency of interactions, particularly adult/juvenile affiliative interactions, during the breeding season at Seer.

7.3.4. Coarseness of interaction assessments

Of the sixteen interactions included in the original ethogram (Chapter 3, Appendix 3.II), only five had a clear enough influence on spatial distribution for inclusion in SNA. Thus, many interactions that could potentially contribute to forming and maintaining social structure, including interpositions and interstallion confrontations, were not included in network analyses. Interactions between adult mares are not common and affiliative interactions in particular are rare and often subtle (Wells and Goldschmidt-Rothschild 1979, Rubenstein 1994). As a result, many studies used proximity to define social bonds between mares (Wells and Goldschmidt-Rothschild 1979, van Dierendonck et al. 2004, Bouskila et al. 2015, Briard et al. 2015, Stanley et al. 2018). Both high frequency interactions and spatial proximity measures capture equid social structure at only a very coarse scale (King et al. 2016). Equids can respond to very slight changes in actual or suggested pressure and the body posture of individuals with whom they are communicating. Thus, probably many, or even most, of the social cues influencing interindividual distance are too subtle to be captured by standard interaction observations or proximity measures. The development of research methodology that could capture more subtle body language would provide fascinating new insight into how intragroup and intergroup relationships are maintained, particularly by adult mares. For now, however, social proximity and high frequency interactions remain the most practical methods for developing a basic understanding of the social structure of study groups for the purposes of managing reintroduced populations.

7.3.5. Sparseness of Hustai data

The paucity of Hustai results due to the sparseness of the data collected has been a common refrain throughout this thesis. For logistical and financial reasons, a reduced amount of time was devoted to the Hustai portion of this study and the resulting datasets often proved insufficient for the methodology used. The lack of clear trends in the Hustai data confirms the challenge of working with a population where incomplete information exists for all the individuals who encountered focal group members (Croft et al. 2008). While significant differences in network centrality by group membership and reproductive state were observed in all three age categories at Hustai, significant differences could usually be explained by the occurrence of one interaction event, or the weather during some observations. For example, DNG had very high affiliative centrality in the breeding season. One of the two days that DNG was observed in the breeding season was the first warm day in May after a week of colder weather. All individuals were shedding and warm, and as a result, during that day of observation mutual grooming occurred at a very high frequency not seen in the groups observed on previous days that week. It was impossible to say whether the high rate of mutual grooming was typical of the group or merely the result of the timing of the observation. In future, a bare minimum of eight hours of observation for personality assessment and 20 hours of focal group interaction hours per network is recommended to obtain networks dense enough for the SNA methods applied in this study.

7.3.6. Correlation between personality and reproductive state

The correlation between personality traits and the age and sex of individuals proved to be a confounding factor in interpreting tests for a significant relationship between personality score and network metrics. Individual takhi sociability and assertiveness scores were significantly correlated with age and sex, which were the two characteristics used to assign reproductive state (Chapter 2, section 2.3.4; Chapter 3, section 3.2.3.4.1). Significant differences in network metrics relative to reproductive state often were reflected in significant differences in network metrics relative to personality score. For the data collected for this study, testing for significant differences in network metrics relative to personality score within reproductive classes would have produced clearer results. For example, having determined that lactating mares had significantly greater centrality in adult/juvenile intragroup agonistic networks, a second test could have been performed to determine if, within the lactating mare class, more social or more assertive mares had greater centrality. However, testing for significant difference in metrics within reproductive classes would have required larger interaction datasets than were available for these analyses.

7.4. Recommendations for takhi population management

As of now, how expanding takhi populations will interact with and integrate into the ecosystems surrounding the current reintroduction sites remains unknown. Management of growing takhi populations will require adaptive strategies informed by constant monitoring of both takhi and the surrounding ecosystem, including wild and domestic animal populations, as well as frequent, more focused, research studies. From the results of this study, it is proposed that the long-term monitoring of male relationships, filly dispersal, and interindividual associations and interactions should be incorporated into future takhi population management strategies.

7.4.1. The importance of monitoring male relationships

Results presented in this thesis suggest that relationships between males as juveniles and as adults influence intergroup cohesive tendencies in takhi family groups. For immediate application of study results, managers should identify stallions with the highest and lowest intergroup proximity tolerance and monitor the results of their encounters with other family groups and with domestic horses. Researchers should also begin tracking the influence of juvenile peer relationships between colts on later relationships as mature family stallions and bachelors.

The gates of the Seer enclosure will be opened once the projected carrying capacity of the fenced area (estimated to be ~100 individuals) is reached (Association pour le cheval de Przewalski: TAKH 2017a). Once the takhi are free to move outside the fence, ideally, they will still use the current reserve as their core area, but it is not possible to know how they will respond to the opening of the gate. Dispersing juveniles, transferring mares, and bachelor stallions who have succeeded in getting outside the fence in the past have travelled up to 100 km from the reserve, and have often been found in the company of domestic horses (TAKH, unpublished data). All individuals were returned to the enclosure by rangers and have since settled into family groups. The Hustai population, although unfenced, is beginning to show signs that the population within the park is reaching carrying capacity, with increasing intraspecific aggression and more frequent dispersal of bachelors outside park boundaries (Kaczensky et al. 2016).

The herd structure observed at Seer, if it continues to persist, would be ideal for minimizing contact with domestic horses and providing dispersers with families or stallions to join without the risk of contact with domestic horses. At both Seer and Hustai, dispersal outside the reintroduction area brings dispersers outside the reach of other takhi as potential social companions and into contact with domestic horses. The results of this study suggest stallion tolerance has the strongest influence on intergroup proximity. Of the stallions, more social and/or more assertive individuals appeared to be the most comfortable with close proximity to other family groups. These results agree with those of Rutberg (1990) and Rubenstein (1994) who found that family stallion age, length of tenure, and dominance were positively correlated with family group stability. Thus, family groups with young and inexperienced stallions or older, senescing stallions would be more apt to show reduced intragroup cohesion, reduced tolerance of intergroup proximity, and potentially increased levels of intra- and intergroup aggression (Berger 1986, Rutberg 1990, Rubenstein 1994). Therefore, the results presented here suggest that monitoring of pre-dispersal colt, bachelor stallion, and family stallion relationships can be used to develop predictions of the potential each stallion has for promoting or causing a breakdown of cohesion between family groups.

7.4.2. The importance of monitoring filly dispersal, domestic horse/takhi co-occurrence, and hybridisation

7.4.2.1. Filly dispersal and domestic horse/takhi co-occurrence

Dispersing fillies present a second challenge to managers, particularly if they frequently travel long distances during their initial dispersal efforts, as observed at Seer. Observations to date suggest that fillies brought back to the takhi population will eventually settle into an established family. As the population grows, unnoticed dispersals could increase the chance of fillies joining a domestic horse stallion. Long term population management plans for takhi reintroductions should include regular patrols of the edges and core of the known takhi range. Regular communication with domestic horse herders in the area should be maintained, so that reintroduction managers can immediately be informed if a dispersing takhi is observed with domestic horse herds. Regular surveys of domestic horse and takhi herd distribution and movement would provide the reintroduction project with information on the range use of domestic herds in areas shared with takhi, improve the chances of predicting interspecific encounters, and help manage takhi groups to reduce encounters. Regular dissemination of domestic horse and takhi distribution data to herders could provide them with valuable herd management information as well. Mongolian domestic horse herds are often allowed to roam freely (van Duyne et al. 2009) and can be challenging for their owners to locate, often requiring an extensive investment of time and money, particularly for vehicle maintenance and petrol. Thus, technology that could provide GPS data on the movement of domestic horses and takhi without interfering with their day-to-day activities and could be disseminated to herders regularly could provide useful rangeland management information to both the reintroduction project and local herders.

7.4.2.2. Recommended prioritisation of a hybrid monitoring programme

Despite ongoing discussion regarding facilitation of greater interproject cooperation among the three Mongolian reintroduction projects, there has been limited progress to date. The establishment of a programme monitoring hybridisation occurrence at all three reintroduction sites would provide critical data regarding the immediate threat posed by interactions between takhi and domestic horses and highlight potential problem areas requiring more active management, if hot spots of hybridisation were found to occur. Given the observed tendency for dispersing fillies to travel long distances and encounter and mate with multiple stallions during their first few oestrous periods (Monard et al. 1996), genetic testing of the foals of primiparous dams should be prioritised by any hybridisation monitoring programme.

7.4.3. Long-term interaction monitoring

The daily monitoring conducted at Seer, and previously at Le Villaret, has resulted in an impressive dataset of information on group location, group membership, and interaction exchanges from 24 years of observations. Daily monitoring at Hustai consists of recording the location, size, composition, and identity of family groups. Long-term monitoring of the reintroduced takhi populations will continue to provide valuable information on the health and viability of individuals and the population, as well as contributing to our knowledge of the natural behaviour of a species not seen in the wild for decades prior to reintroduction. Detailed monitoring will become more challenging as reintroduced populations grow. Each new generation becomes more challenging to identify and observe. At Hustai now, many young takhi do not receive names or studbook numbers for several years, but are instead identified by their mother's name and their current age (HNP, unpublished data). Future monitoring needs to adapt and prioritise methods that balance high quality data collection with financial and logistical constraints. Development and application of long distance or passive monitoring methods would be ideal, as data could be gathered regardless of terrain and weather. Basic data to continue collecting for long-term monitoring in growing populations would include weekly to daily monitoring of the position, identity, and composition of all family and bachelor groups, and the location of all lone takhi. Focal group interaction observations will be more challenging to continue implement as populations grow but, with a clearly defined ethogram and trained observers, would continue to provide valuable information regarding the contribution of individuals and interindividual interactions to overall social structure.

Tong et al. (2015) found a significant tendency for adult mares occurring in the same herd to be related, while the same tendency was not observed for stallions. Similar trends were not observed at Seer (relatedness data were not available at Hustai), but the population is small, with relatively high relatedness overall, so it is probably too soon to be able to detect any trends in herd level cohesion relative to relatedness. Future monitoring efforts should investigate the influence of relatedness on herd cohesiveness.

7.5. Suggestions for further research

The analyses conducted for this study represent only the beginning of the analyses possible for this dataset and for further investigation into mechanisms of takhi social cohesion. Some initial suggestions regarding further research are as follows.

7.5.1. Investigation of the role of long term relationships on social structure

From this study it appears that in takhi perception of familiarity has nuances beyond natal group or current group co-membership as was applied in this study and others (Duncan et al. 1984, Berger and Cunningham 1987, Monard et al. 1996). Further research should investigate factors influencing recognition of conspecifics in takhi, and the influence of varied levels familiarity on family group and herd cohesion. Studies should also explore the influence of juvenile intermale relationships on adult stallion intergroup proximity tolerance and cohesive tendencies.

7.5.2. Assessment of group and herd synchrony

In addition to proximity, synchronization of behaviour is considered the other main metric by which group cohesion can be measured (Conradt and Roper 2000, King et al. 2016). During the collection of spatial data for this study, the behaviour state of each individual was also recorded (see Chapter 3, section 3.2.1.2.2). The state data collected could be used to compare intragroup and intergroup state synchronization at Seer and Hustai relative to spatial distribution. Behaviour state filters could also be applied to the spatial data. For example, differences in centrality among different reproductive classes or personality types could be tested, comparing periods when >75% of the group or herd is grazing versus when >75% of the group or herd is resting.

7.5.3. Further work with interaction networks and personality assessment using expanded datasets

Both interaction SNA and personality assessment should be repeated using larger datasets to determine if the trends observed in this study are reproducible. With larger interaction datasets, within-reproductive class tests for significant difference in interaction network metrics relative to personality type could be performed. In addition to, or instead of, gathering additional interaction data, SNA of the interaction data existing in the TAKH database could also be performed with the same aim.

7.5.4. Tests using pre-network permutation methods

Both spatial and interaction SNA should be repeated using the pre-network data permutation methods discussed in section 7.3.1.2. The results could then be compared to those from post-network permutation methods.

7.5.5. Development of different methods for measuring spatial distribution

The spatial distribution methods applied in this study (Chapter 3, section 3.2.1.2.2), although resulting in an extremely detailed dataset, were intensive and would be impractical to include as part of long-term monitoring efforts. To date, GPS tracking technology has only been applied at the GGB takhi reintroduction site, where a few takhi were collared to obtain data on home range and habitat use (Kaczensky et al. 2008, 2013). For collecting finer scale data, such as interindividual distance measures, collars would have to be attached to all individuals in all focal groups. GPS collars have not been extensively applied in takhi population monitoring as the physical (to the takhi) and logistical and financial (to the humans) costs usually outweigh the benefits of the quality of data obtained. There are also concerns of collars interfering with or inaccurately recording natural behaviour (Brooks et al. 2008, Owen et al. 2012; C. Hall, pers. comm. 2017). As remote tracking technology continues to develop, improved alternatives for monitoring fine scale spatial positioning are sure to become available (Lopez-Lopez 2016, Meyer 2017). An ideal solution for long-term monitoring of takhi spatial distribution and group membership would be a device similar to a PIT (passive inductive transponder) tag that could be injected from a distance using a dart gun, and then scanned by a device (perhaps handheld or drone) that could more quickly and efficiently capture both distance and angle to study animals in the same manner as the rangefinder used in this study.

7.5.6. Development of methods for assessing fine scale social cues

As discussed above, many exchanges between horses which influence social relationships and spatial distribution cannot be captured at the scale of interval measurements of interindividual distance or rate of high occurrence interactions (King et al. 2016). Further work developing methods for identifying relevant non-contact and low intensity interactions may provide greater insight into behavioural mechanisms of takhi cohesion. Possible avenues to explore could include analyses of approach and retreat events between individual takhi. Prior to one takhi moving out of the path of another, what facial or body language was displayed by both? At what distance between individuals is a mild or more intense agonistic response elicited? Is that distance consistent among individuals of differing reproductive state or personality? Under what circumstances is an affiliative response invoked, rather than an agonistic one? Investigation into how takhi use finer scale body language and social cues to manage social relationships and spatial distribution would not only benefit studies of takhi social structure, but would also be applicable to management of feral and domestic horse populations, and could be applied to improve horse/human communication as well.

7.6. Conclusion

The main outcomes of this study are as follow. This study:

- developed methodology for measuring the spatial position of all individuals in a herd of >50 takhi across multiple time steps,

- developed and applied two field-based methods of assessing personality in free-living takhi populations,
- determined that some family groups may occupy spatial broker positions in takhi herds,
- found that mildly social takhi tended to be peripheral in intergroup spatial networks,
- found that males were significantly more active than females in intergroup affiliative networks
- found that stallions were significantly more active than other reproductive classes as the managers of intergroup borders, and
- found that mares were significantly more active than other reproductive classes as the managers of intragroup spatial distribution.

The purpose of this study was to identify potential mechanisms of social cohesion within and between family groups of reintroduced takhi. The results of the analyses presented here provide suggestions of mechanisms of cohesion, but do not claim a final and definitive answer. Results suggest that stallion relationships have a major influence on intergroup cohesion levels. Personality type may have a significant influence on individual proximity to other family groups, but more research is required. Within groups, adult mares appear to manage spatial and social structure. Previous research has suggested that mares remain in family groups to maximise their access to the food resources necessary to support themselves and their nutritionally dependent offspring, while stallions remain in family groups to maximise their access to mares (Rubenstein 1994, Linklater et al. 1999, Tong et al. 2015). Perceived accessibility of necessary resources can be expected to influence cohesion (Conradt et al. 2009). Mares who feel their access to resources is threatened can be expected to reduce that threat by increasing interindividual distance. Stallions who feel their access to mares is threatened can be expected to reduce that risk by increasing intergroup distance. The centrality of mares in intragroup networks and the centrality of stallions in intergroup networks supports these expectations. At both Seer and Hustai, adults of both sexes appear to be most active in managing interindividual proximity. Mares do so more at the family group level, while stallions are more active at levels above that of the family group. It seems most likely that intergroup affiliative interactions are facilitated by the close proximity of other groups, rather than vice versa, but it’s possible that frequent intergroup play between juveniles could contribute to higher tolerance of closer intergroup proximity as adults.

This study has explored the role that different individuals play in the formation of takhi intragroup and intergroup social structure. The information presented here is intended to further our understanding of the mechanisms by which socially natural groups of takhi are maintained, and how that understanding can be applied to the management of reintroduced takhi populations and of other equids with similar social structure.

8. References

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9. Appendices

Appendix 2.I: Rater assessment of personality, draft

Przewalski's Horse Descriptors/ Тахь тодорхойлолт

Horse Name/ Тахын Нэр: ____________________ Horse ID/ Тахын ID: _______
Name/ Нэр: _________________________
How many months (years) have you observed this horse? / Та хэдэн сар (жил) энэ тахь харсан бэ? ________________
What years did you observe this horse? / Аль он энэ тахь харсан уу? _________________

Below are pairs of words joined by a dotted line. Please mark on the line the point you feel best describes this horse. For example, a fairly smart horse would be scored as;

Доорхи цэгэн зурээсэнд уг тахь нь эль тодорхойлолтонд илүү ойр байгааг тэмдэглэнэ үү. Жишээ нь: үнэхээр ухаантай тахь;

Example/Жишээ

smart/ухаантай	………X…………………………………………………………	stupid/тэнэг

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experienced / туршлагатай	…………………………………………………………………...	inexperienced / туршлагагүй
bad character / ааш муутай	…………………………………………………………………...	good character / ааш сайтай
social / ниитэч	…………………………………………………………………...	antisocial / хажиг, зожиг
follower / дагалдагч	…………………………………………………………………...	leader / удирдагч
alert/vigilant / сонор сэргэг	…………………………………………………………………..	not sensitive/vigilant / сонор сэргэг биш
bold / зоригтой	…………………………………………………………………...	shy / ичимхий
tame / догшин биш	…………………………………………………………………...	wild / догшин

submissive / номхон даруу	………………………………………………………………………..	dominant / давамгайлагч
smart / ухаантай	………………………………………………………………………..	stupid / тэнэг
playful / тоглох дуртай	………………………………………………………………………..	not playful / тоглох дургүй
stoic / тэвчээртэй, тэсвэртэй	………………………………………………………………………..	weak / сул дорой
calm / тайван/дөлгөөн	………………………………………………………………………..	excitable/nervous / түгшсэн/хөөрүү
lazy / залхуу	………………………………………………………………………..	active / идэвхтэй
permissive / зөөлөн хүлцэнгүй	………………………………………………………………………...	domineering/controlling / дээрэлхүү, захирангүй
grazes at edge of herd / сүргийн захаар явах дуртай	………………………………………………………………………..	grazes at centre of herd / сүргийн төвөөр явах дуртай
grazes at front of herd / сүргийн эхэнд явах дуртай	………………………………………………………………………..	grazes at back of herd / сүргийн ар талд явах дуртай

Appendix 2.II: Ethogram for behaviour scan samples

1. Approach human - With head up and ears pricked, takhi moves towards human.
2. Autogroom – Takhi scratches, rubs, or bites self.
3. Autogroom with object - Takhi rubs any part of body on some other object.
4. Backing - Takhi moves backwards at a steady rate.
5. Bite – Takhi's mouth closes on some part of a conspecific's body.
6. Bite threat – Takhi moves head and neck, open mouthed, towards conspecific, but does not make contact.
7. Blocking – Foal moves in front of dam to block her progress and allow nursing.
8. Bold approach (conspecific) - Takhi approaches another individual with no visible hesitation and no submissive behaviours.
9. Charge – Takhi lunges towards conspecific for one stride, with mouth open or closed, with ears back.
10. Chase – Takhi lunges towards conspecific and follows for more than one stride at a run, with mouth open or closed, with ears back, frequently turning its head toward the conspecific.
11. Chasing conspecific – Takhi follows conspecific for more than one stride of trot or gallop, driving off by head threats, bite threats, and bites.
12. Chewing - Takhi stands and chews a mouthful of food.
13. Chewing object – Takhi visibly used teeth to grasp, scrape, or grind an object.
14. Cough - Takhi coughs.
15. Defecating – Takhi defecates.
16. Dominant approach (conspecific) – Takhi approaches conspecific at a distance of < 50 metres, at a steady to brisk pace (fast walk, trot, or canter), head up and ears forward.
17. Drinking/eating snow – Takhi consumes water, or takes bites of snow.
18. Driving conspecific - Takhi moves directly behind conspecific using body language to direct the conspecifics movement, but does not assume herding posture.
19. Fleeing conspecific – Takhi retreats at a trot or gallop from a charge or chase by conspecific.
20. Flehmen - Takhi stands with upper lip curled in flehmen position.
21. Following conspecific - Takhi moves slowly behind conspecific, not chasing. Head threats may or may not be visible.
22. Grazing – Takhi takes bites of grass or chews. May be walking or standing still. Head is below the level of the withers and takhi is not focused on stimuli > 5 metres away.
23. Groom conspecific – Takhi scratches or rubs a conspecific's body with lips or teeth.

24. Head threat – Takhi pins ears and snakes head/neck toward conspecific.
25. Head toss (fly control) - Takhi moves head up and down in a rapid repetative motion to disperse insects.
26. Herding – At a walk, trot, or gallop, with ears back and head lowered (snaking), takhi drives one or several conspecifics in front of it. Not accompanied by biting, as would be seen with a chase.
27. Hesitant approach (conspecific) - Takhi approaches conspecific at a distance of < 50 metres slowly, or obliquely, frequently checking for a reaction from conspecific.
28. Interposition – Takhi moves between two conspecifics engaged in an interaction.
29. Investigate object – Takhi visibly focuses on and/or sniffs an object < 5 metres away.
30. Kick – Takhi extends one or both back legs toward conspecific, either making contact or fully extending one or both legs.
31. Kick threat – Takhi threatens to kick conspecific by turning rump to conspecific with tail clenched, and may or may not raise one or both back legs and partially extend them, but does not make contact with conspecific's body.
32. Lateral Rest - Takhi lies down with shoulder, hip, and side of head resting on ground. Eyes may be closed or open.
33. Lying down - Takhi is in the process of lowing body to ground.
34. Mating – Stallion mounts mare with intromission.
35. Mating attempt – Stallion mounts mare, but with no intromission.
36. Missed – Observer does not record takhi during scan.
37. Mutual fly control – Takhi stands head to tail with another takhi for the purpose of removing flies from partner, and having flies removed by partner.
38. Nursing – Foal suckles on mother's teat.
39. Other - Any other observed behaviour.
40. Other contact with conspecific – Any other body contact between takhi and conspecific.
41. Other vocalization - Any quiet vocalization; nicker, grunt, sigh, etc.
42. Out of sight – Takhi cannot be seen by the observer.
43. Pawing – Takhi lifts foreleg off ground, extends it quickly forward, and then drags it backward with the toe in contact with the ground, but not directed toward another takhi (McDonnell, 2003).
44. Play bite - Takhi mouths or bite conspecific, with ears not pinned.
45. Play chase - Takhi follows conspecific for more than one stride of trot or gallop, driving off by bite threats, and bites. Ears are not pinned.

46. Play fight – A series of bites, kicks, bite and kick threats, and rears. The ears of the takhi are not pinned.
47. Play flee - Takhi retreats at a trot or gallop from a charge or chase by conspecific, may kick, bite, or bite threat. Ears not pinned.
48. Play kick - Takhi kicks conspecific during a play session or at rest. Ears not pinned.
49. Play mount - Takhi rears on hind legs and rests chest and/or forelegs on the rump, back, or neck of conspecific.
50. Play other - Any other behaviour occurring during a play session.
51. Rear – Takhi stands on hind legs.
52. Retreat from conspecific - Takhi visibly moves away from conspecific as a result of conspecific's gesture or expression.
53. Retreat from human - Takhi visibly moves to avoid human.
54. Resting standing – Takhi stands in a relaxed position (eyes closed or half closed, one leg cocked, ears relaxed) with no visible focus (pricked ears, head up) on external stimuli.
55. Rolling – Takhi lies down and rubs head/neck on the ground, turns over halfway, or rolls all the way over.
56. Running – Takhi moves at a gait faster than a trot.
57. Shake - Takhi shakes.
58. Snapping – Takhi makes a submissive mouthing gesture (opening and closing its jaws several times) towards dominant conspecific.
59. Sniff conspecific – Takhi touches its nose to any part of a conspecific's body.
60. Sniff dung - Takhi deliberately moves nose to a close proximity with dung pile and inhales.
61. Sniff ground – With no other object visibly present, takhi lowers nose to the ground.
62. Sniff object - Takhi deliberately moves nose to a close proximity with an object and inhales.
63. Spook - Takhi suddenly arrests movement or changes direction of movement in response to the presence of some stimuli.
64. Standing up - Takhi stands up from recumbent position.
65. Stallion confrontation – Stallions exchange bites and kicks, rearing and bucking. A confrontation is over when one stallion leaves the meeting place.
66. Stallion display – Stallions paw, arch necks, sniff and circle each other. A display is over when one stallion leaves the meeting place or the interaction progresses to a confrontation.

67. Stallion ritual – Stallions, one alone, or multiple, deposit dung and sniff it. May paw the ground.
68. Sternal Rest - Takhi lies down with chest resting on ground, and head up (not touching the ground). Eyes may be closed or open.
69. Stretching – Generally after resting, takhi stretches some part of the body (neck, back legs, forelegs etc.).
70. Strike – Takhi raises and extends foreleg toward another takhi, rapidly and aggressively, with ears back. May or may not vocalise.
71. Submissive approach - Takhi approaches conspecific at a distance of < 50 metres, and displays snapping.
72. Trotting – Takhi moves at a trot (two beats).
73. Urinating – Takhi urinates.
74. Vocal Approach – Takhi (usually a stallion) approaches another takhi (usually a mare) while vocalizing (sometimes starts as a neigh or squeal but generally ends as a nicker) (Seer definition).
75. Vocalization – Takhi neighs, squeals, or whickers in any context besides a vocal approach.
76. Walking – Takhi moves at a walk (four beats) and is not pausing to bite grass.
77. Watching conspecific – Takhi stands still, with head up, ears pricked forward, focused on another takhi.
78. Watching human – Takhi stands still, with head up, ears pricked forward, focused on observer or another human.
79. Watching other – Takhi stands still, with head up, ears pricked forward, focused on some external stimuli.
80. Yawning - Takhi yawns.

Appendix 3.I: Glossary of social network analysis terms as they are used in this thesis. All words listed are also defined and discussed in detail in the text. Words highlighted in bold within the definitions below are themselves words defined in the glossary.

Association – A relationship between two individuals that would be recorded as a **link** in a **network sociogram** or matrix. Individuals are considered associated when they occur in the same group or together within a defined area. Associations often serve as a way to define a relationship between two individuals when actual interactions between individuals are too difficult to observe and record (Whitehead 2008a).

Association index – The method used to estimate the proportion of time that two individuals are associated (Cairns and Schwager 1987, Whitehead 2008a).

Association matrix – A matrix of association relationships (as opposed to interaction relationships).

Attribute(s) – The characteristics of individual **nodes**, which can include demographic characteristics such as age, sex, or personality or node level metrics such as **degree** or **betweenness**.

Betweenness – A **node metric** that measures the number of shortest paths between all other nodes that pass through the node of interest (Croft et al. 2008).

Binary network – A **network** where **links** are either present (with a **weight** of one) or absent.

Clustering coefficient – A **node metric** that describes the extent to which the immediate **neighbours** of a **node** are also connected to each other.

Degree – A **node metric** that describes the number of connections an individual has to other individuals in the **network**.

Directed network – A **network** in which a **link** given by individual A and received by individual B may or may not also be given by B and received by A, (or may still occur, but with a different **link weight**).

Dyad – A pair of individuals.

Indegree – A **node metric** that describes the number of **links** received by an individual in a **directed network**.

Instrength – A **node metric** that describes the summed **weight** of all **links** received by an individual in a **directed network**. Only applicable to **weighted networks**.

Interaction – An action of one individual directed towards or affecting the behaviour of another (Whitehead 2008a).

Interaction network – A **network** in which connections are formed by **interactions** occurring between individuals. Usually **directed**.

Link(s) – The relationship between two individuals which connects them in an **association**, **spatial**, or **interaction** network. Also known as 'edge(s)', 'tie(s)', 'connection(s)', or 'arc(s)'.

Metrics – Unless specified otherwise, metrics in this thesis refer to **node**-level **network** metrics. Metrics describe the position, and to an extent the role, of individual **nodes** in the network.

Neighbour(s) – The **node(s)**/individual(s) in a **network** directly connected by a **link** to the **node**/individual of interest.

Network – A dataset consisting of **nodes** connected by **links**. Usually a network will represent one population and/or study period.

Node(s) – The actors in a **network**. Displayed as a point in the visualisation of a network, nodes usually represent individual animals when used in animal social network analysis (Croft et al. 2008).

Outdegree – Synonymous with **degree**, but sometimes used instead for increased clarity. Only used in reference to **directed networks**.

Outstrength - Synonymous with **strength**, but sometimes used instead for increased clarity. Only used in reference to **directed networks**.

Sociogram – A visual depiction of a **network** in which **nodes** are drawn as points and **links** are drawn as lines connecting the points where relationships occur.

Spatial network – A **network** in which the **links** between individuals represent the physical distance between them. The term is specific to this study.

Strength – The sum of the **weights** of all **links** connected to the **node** of interest. In **binary networks**, strength is equal to **degree**.

Triplet – A group of three **nodes** connected by at least two **links** in an **undirected network**. A triplet with three **links** is a 'closed triplet,' while a triplet with two **links** is an 'open triplet.'

Triplet value – For this study, the average of all **link weights** in the triplet of interest.

Undirected network – A **network** where the **link weight** from individual A to individual B is always the same as that from B to A.

Weight – The value of a **link** in a **network**. In **binary networks** the weight always equals one. In **weighted networks**, the **link's** weight represents the strength of the relationship between the **nodes** it connects.

Weighted network – A **network** in which each **link** has a numeric value with represents the strength of the relationship between **nodes**.

Appendix 3.II: The characteristics of the takhi in the focal family groups at Seer and Hustai

Table 3.II. 1. The characteristics of the Seer takhi. Within the personality score headings, C = the continuous personality score and D = the discrete personality score (see Chapter 3, section 3.2.3.4.2). NC indicates that a score could not be calculated.

ID	Focal group membership		Reproductive state		Assertiveness		Sociability	
	Non-breeding	*Breeding*	*Non-breeding*	*Breeding*	*C*	*D*	*C*	*D*
AH	DIG	DIG	Non-reproductive mare	Non-reproductive mare	2.94	4	1.68	5
AR	BRG	BRG	Non-reproductive mare	Non-reproductive mare	4.28	2	2.74	4
AS	CRG	CRG	Non-reproductive mare	Non-reproductive mare	4.18	2	2.5	4
BG	OTHER	OTHER	Non-reproductive mare	Non-reproductive mare	4.01	2	3.02	3
BI	DIG	DIG	Colt	Colt	2	5	4.07	2
BR	BRG	BRG	Mature stallion	Mature stallion	3.79	3	1.46	5
CA	BRG	BRG	Reproductive mare	Reproductive mare	4.61	2	3.66	3
CH	DIG	DIG	Non-reproductive mare	Non-reproductive mare	NC	NC	NC	NC
CI	DIG	DIG	Reproductive mare	Reproductive mare	2.74	4	0.54	6
CL	CRG	CRG	Reproductive mare	Reproductive mare	4.3	2	3.46	3
CM	DIG	DIG	Reproductive mare	Reproductive mare	3.51	3	3.34	3
CR	CRG	CRG	Mature stallion	Mature stallion	5.32	1	2.34	4
DB	CRG	CRG	Non-reproductive mare	Non-reproductive mare	5.16	1	4.87	2
DI	DIG	DIG	Mature stallion	Mature stallion	3.82	3	3.34	3
GA	CRG	BRG	Filly	Filly	2.88	4	2.56	4
GH	DIG	DIG	Reproductive mare	Reproductive mare	NC	NC	NC	NC
HA	DIG	DIG	Colt	Colt	2.61	4	3.46	3
HS	DIG	DIG	Colt	Colt	1.95	5	3.84	3

KD	DIG	DIG	Reproductive mare	Reproductive mare	3.21	3	0.9	6
KH	CRG	CRG	Reproductive mare	Reproductive mare	3.22	3	2.39	4
KL	BRG	BRG	Reproductive mare	Reproductive mare	3.1	3	3.99	3
LI	DIG	DIG	Reproductive mare	Reproductive mare	3.02	3	0.23	6
NA	CRG	CRG	Colt	Colt	2.68	4	4.01	2
NI	BRG	OTHER	Filly	Filly	1.6	5	2.51	4
PX	BRG	OTHER	Colt	Colt	2.24	4	3.15	3
SH	BRG	BRG	Reproductive mare	Reproductive mare	3.43	3	2.6	4
SR	CRG	CRG	Reproductive mare	Reproductive mare	4.29	2	2.73	4
SS	BRG	BRG	Reproductive mare	Reproductive mare	NC	NC	NC	NC
TA	BRG	OTHER	Filly	Filly	3.34	3	3.07	3
TO	BRG	OTHER	Colt	Colt	1.55	5	3.67	3
UH	BRG	BRG	Reproductive mare	Reproductive mare	3.19	3	3.15	3
UL	DIG	DIG	Colt	Colt	1.87	5	2.88	4
VE	CRG	BRG	Filly	Filly	2.5	4	2.98	4
YO	DIG	OTHER	Colt	Colt	3.64	3	4.54	2

Table 3.II. 2. The characteristics of the Hustai takhi. NA indicates the individual takhi wasn't present during that season.

ID	Family group membership		Reproductive state	
	Non-breeding	*Breeding*	*Non-breeding*	*Breeding*
BD0	BDG	BDG	Mature stallion	Mature stallion
BD1	BDG	*NA*	Colt	*NA*
BD2	BDG	BDG	Reproductive mare	Reproductive mare
BD4	BDG	BDG	Reproductive mare	Reproductive mare
BD6	BDG	BDG	Reproductive mare	Reproductive mare
BD7	BDG	BDG	Reproductive mare	Reproductive mare
BD8	BDG	*NA*	Colt	*NA*
BD9	BDG	BDG	Reproductive mare	Reproductive mare
BD10	BDG	*NA*	Colt	*NA*
BD12	BDG	BDG	Colt	Colt
DN0	DNG	DNG	Mature stallion	Mature stallion
DN1	DNG	DNG	Reproductive mare	Reproductive mare
DN2	DNG	DNG	Reproductive mare	Reproductive mare
DN3	DNG	DNG	Non-reproductive mare	Non-reproductive mare
DN4	DNG	DNG	Reproductive mare	Reproductive mare
DN5	DNG	DNG	Filly	Filly
DN6	DNG	DNG	Filly	Filly
DN7	DNG	DNG	Colt	Colt
DN8	DNG	DNG	Filly	Filly
DN9	DNG	DNG	Filly	Filly
DN10	DNG	DNG	Reproductive mare	Reproductive mare
KE0	KEG	KEG	Mature stallion	Mature stallion
KE1	KEG	*NA*	Reproductive mare	*NA*
KE2	KEG	KEG	Reproductive mare	Reproductive mare
KE3	KEG	KEG	Filly	Filly
KE4	KEG	KEG	Reproductive mare	Reproductive mare
KE5	KEG	KEG	Reproductive mare	Reproductive mare
KE7	KEG	KEG	Reproductive mare	Reproductive mare
KE9	KEG	KEG	Filly	Filly
WN0	WNG	WNG	Mature stallion	Mature stallion
WN1	WNG	WNG	Reproductive mare	Reproductive mare
WN2	WNG	WNG	Colt	Colt
WN3	WNG	WNG	Reproductive mare	Reproductive mare
WN4	WNG	WNG	Filly	Filly

ZR0	ZRG	ZRG	Mature stallion	Mature stallion
ZR1	ZRG	ZRG	Non-reproductive mare	Non-reproductive mare
ZR2	ZRG	ZRG	Non-reproductive mare	Non-reproductive mare
ZR3	ZRG	ZRG	Non-reproductive mare	Non-reproductive mare
ZR4	ZRG	ZRG	Colt	Colt
ZR5	ZRG	ZRG	Reproductive mare	Reproductive mare
ZR6	ZRG	*NA*	Non-reproductive mare	*NA*

Appendix 3.III: Ethogram for interindividual interactions at Seer and Hustai

Definitions in **bold** are directly transcribed from the Seer ethogram (Feh 2012b).

Head Threat/Bite Threat/Bite Attempt - A ears back, mouth open, turns head and/or neck towards D. There may be physical contact between A's teeth and D's body (a bite) or not. A and/or D can be standing, walking, grazing, or lying (Feh 2012b).

Kick Threat – A, ears back, turns its hindquarters towards D, or A ears back, lifts one or two hind legs in D's direction without or only partially extending them. A may or may not back towards D. A's hoofs may or may not touch D's (Feh 2012b).

Kick - A, ears back and both hind legs off the ground, strikes out towards D. A's hooves may or may not touch D's body (Feh 2012b).

Strike – A, often squealing, lifts one foreleg and puts it back on the ground immediately. Sometimes both forelegs are lifted in a rapid succession, but never simultaneously (Feh 2012b).

Vocal Approach - A, generally a stallion, approaches D, generally a mare. A is vocalizing (nicker). Sometimes the vocalization starts with a whinny or a squeal, but always ends in a nicker. The stallion often arches his neck (Feh 2012b).

Charge – A, ears back, mouth open or closed, trotting or galloping towards D in one rapid motion, turns head and/or neck towards D once. There may or may not be physical contact between A's teeth and D's body (Feh 2012b).

Chase – A, ears back, galloping towards D, turns head and/or neck towards D several times. A's mouth can be open or closed. There may be physical contact between A's teeth and D's body (a bite) or not (Feh 2012b).

Herding – A, generally a stallion, ears back, head and neck extended in one line below the horizontal of its back, trots or gallops towards D(s) (Feh 2012b). A new 'herding' is record after A makes a different interaction or A herds a different individual(s).

Stallion Ritual – Stallion A approaches or is approached by D. Includes head bowing, olfactory investigation, posturing, parallel prance, dung display, dung sniff, pawing, head bumping, pushing, striking, or squealing (McDonnell 2003). Stallion A or D then retreats.

Stallion Confrontation – If the stallion A or D does not retreat and interactions progress to include bites, kicks, rears, charges or chases, the interaction becomes a stallion confrontation.

Mutual Groom –A and D scratch each other's skin mutually and rhythmically (ca 2 times/sec) with their incisors. Interaction is recorded following the third mutual scratch. If interactors change sides or locations during the grooming sequence, still recorded as one interaction (Feh 2012b).

Play – Individuals A and D directs a play version of a bite, kick/kick threat, rear, or chase towards D (McDonnell 2003). Play versions of interactions are distinguished from 'serious' interactions by the position of the ears (forward or sideways) and the expressions of the interactors.

Snapping - A makes several rapid vertical jaw movements, with lips retracted. This interaction can occur as a reaction to an interaction, or as A approaching D and snapping (Feh 2012b).

Interposition – During an interaction between A and D, C puts its head or body between A and D. C can approach A and D from front or behind. C may or may not interact with A or D (Feh 2012b).

Interaction Response – Move away – D moves at least one step away from A immediately after the interaction. D may be walking, trotting, or galloping (Feh 2012b).

Interaction Response – No Reaction – D stays immobile immediately after interaction with A (Feh 2012b).

Appendix 3.IV: Example of RStudio code used to generate observed network metrics at Seer and Hustai. This example shows the code for calculating network metrics for juvenile intergroup spatial and affiliative interaction networks at Seer for analyses presented in Chapter 5. To apply the code to different networks, input and output file names are changed depending on the season and location for which metrics are being generated. Any line of code preceded by '#' indicates instructions or description, rather than actual code.

```
library(tnet)
Attribute<-JuvenileAttributes

#################################
##Juvenile Intergroup Distance##
#################################

Network<-as.tnet(JuvInter, type="weighted one-mode tnet")
Network<-symmetrise_w(Network,method="MAX")
#To calculate non-directed or out degree with alpha = 0.5
patch<-Attribute[c("NumberID","ID")]
node<-patch$NumberID
patch<-cbind(patch,node)
deg_w<-degree_w(net=Network, measure=c("degree","output","alpha"),
      alpha=0.5)
deg1<-data.frame(deg_w)
patch<-merge(patch,deg1,by="node",all=TRUE)
patch[is.na(patch)]<-0
Attribute$JuvInter_strength<-patch$output
Attribute$JuvInter_degreeA0.5<-patch$alpha
patch<-Attribute[c("NumberID","ID")]
node<-patch$NumberID
patch<-cbind(patch,node)
bet_w<-betweenness_w(Network, alpha=1.5)
bet1<-data.frame(bet_w)
patch<-merge(patch,bet1,by="node",all=TRUE)
patch[is.na(patch)]<-0
Attribute$JuvInter_between<-patch$betweenness
patch<-Attribute[c("NumberID","ID")]
node<-patch$NumberID
patch<-cbind(patch,node)
clust<-clustering_local_w(Network, measure="am")
clust1<-data.frame(clust)
patch<-merge(patch,clust1,by="node",all=TRUE)
patch[is.na(patch)]<-(-0.05)
Attribute$JuvInter_cluster<-patch$am

############################################
##Juvenile Intergroup Affiliative Metrics##
############################################

Network<-as.tnet(SeerJuvenileInterAffiliative, type="weighted one-mode
      tnet")
#To calculate non-directed or out degree with alpha = 0.5
patch<-Attribute[c("NumberID","ID")]
node<-patch$NumberID
patch<-cbind(patch,node)
deg_w<-degree_w(net=Network, measure=c("degree","output","alpha"),
      alpha=0.5)
deg1<-data.frame(deg_w)
patch<-merge(patch,deg1,by="node",all=TRUE)
patch[is.na(patch)]<-0
Attribute$JuvInterAff_strength<-patch$output
Attribute$JuvInterAff_degreeA0.5<-patch$alpha
patch<-Attribute[c("NumberID","ID")]
node<-patch$NumberID
```

```
patch<-cbind(patch,node)
deg_w<-degree_w(net=Network, measure=c("degree","output","alpha"),
      type="in", alpha=0.5)
deg1<-data.frame(deg_w)
patch<-merge(patch,deg1,by="node",all=TRUE)
patch[is.na(patch)]<-0
Attribute$JuvInterAff_instrength<-patch$output
Attribute$JuvInterAff_indegreeA0.5<-patch$alpha
patch<-Attribute[c("NumberID","ID")]
node<-patch$NumberID
patch<-cbind(patch,node)
Network2<-symmetrise_w(Network, method="SUM")
bet_w<-betweenness_w(Network2, alpha=1.5)
bet1<-data.frame(bet_w)
patch<-merge(patch,bet1,by="node",all=TRUE)
patch[is.na(patch)]<-0
Attribute$JuvInterAff_between<-patch$betweenness
patch<-Attribute[c("NumberID","ID")]
node<-patch$NumberID
patch<-cbind(patch,node)
clust<-clustering_local_w(Network2, measure="am")
clust1<-data.frame(clust)
patch<-merge(patch,clust1,by="node",all=TRUE)
patch[is.na(patch)]<-(-0.05)
Attribute$JuvInterAff_cluster<-patch$am

########################################################################
##Print new attribute##
########################################################################
write.csv(Attribute,"JuvenileAttributeMetrics.csv")
```

Appendix 3.V: Example of RStudio code used to test for a significant difference in network metrics (betweenness, strength, degree, instrength, indegree, and clustering coefficient) relative to attribute class at Seer and Hustai. This example shows the code for comparing betweenness and strength scores in the adult intragroup agonistic breeding season network at Seer among individuals of differing family group membership for analyses presented in Chapter 4. To apply the code to different networks, input and output file names were changed depending on the season, location, and age group for which metrics were being compared. Any line of code preceded by '#' indicates instructions or description, rather than actual code.

```
########################################################################
#BIntraAgo vs Group with betweenness
########################################################################
##Initial values to load if not already done for previous analyses
library(tnet)
P<-5000 #Number of permutations
net<-as.tnet(SeerBreedingIntraAgonistic, type="weighted one-mode tnet")
attribute<-BreedingAdultAttributeMetrics

##load conover.test and kruskall.wallis package
library(conover.test)

#create grouping vector
groupvec<-factor(attribute$Group)
metricvec<-attribute$BIntraAgo_between

#Run permutations with node permutation
#calculate observed test stat
cnet<-symmetrise_w(net,method="SUM")
H_obs<-conover.test(metricvec,groupvec,method="by",table=FALSE)$chi2
obspairs<-conover.test(metricvec,groupvec,method="by",table=FALSE)$T
paircomp<-conover.test(metricvec,groupvec,method="by",
      table=FALSE)$comparisons
observedpairs<-data.frame(paircomp,obspairs)

#Create output matrix of pairwise comparisons
#c is number of pairs being compared as gathered from observedpairs file
c<-6
pairsmatrix<-matrix(0,nrow=c,ncol=P)
rownames(pairsmatrix)<-paircomp
random2<-rep(1:P)

#create sna matrix for randomization
library(sna)
snanet <- as.matrix(cnet)
N <- max(c(snanet[,"i"],snanet[,"j"]))
g <- matrix(data=0, nrow=N, ncol=N)
g[snanet[,c("i","j")]] <- snanet[,"w"]
snanet2<- as.sociomatrix.sna(g)

#Runn Conover-Iman's test for random networks

for (i in c(1:P)) {
  rand_df<-attribute[c("NumberID","ID")]
  node<-rand_df$NumberID
  rand_df<-cbind(rand_df,node)
  randnet<-rmperm(snanet2)
  metricrand<-betweenness_w(randnet, alpha=1.5)
  metricrand2<-data.frame(metricrand)
  rand_df<-merge(rand_df,metricrand2,by="node",all=TRUE)
```

```
  rand_df[is.na(rand_df)]<-0
  Randmetricvec<-rand_df$betweenness
  random2[i]<-conover.test(Randmetricvec,groupvec,method="by",
      table=FALSE)$chi2
  pairsmatrix[,i]<-conover.test(Randmetricvec,groupvec,method="by",
      table=FALSE)$T}

NAomit<-sum(is.nan(random2))
random3<-na.omit(random2)
pairsmatrix2<-t(na.omit(t(pairsmatrix)))
upperp<-sum(H_obs<random3)/P
lowerp<-sum(H_obs>random3)/P
absp<-sum(abs(H_obs)<abs(random3))/P
randmean<-mean(random3)
randmedian<-median(random3)
randsd<-sd(random3)

pairpvalue<-rep(1:c)
for(i in c(1:c)) {
  pairpvalue[i]<-sum(abs(obspairs[i])<abs(pairsmatrix2[i,]))/P}
pairmean<-rep(1:c)
for(i in c(1:c)) {
  pairmean[i]<-mean(pairsmatrix2[i,])}
pairmedian<-rep(1:c)
for(i in c(1:c)) {
  pairmedian[i]<-median(pairsmatrix2[i,])}
pairsd<-rep(1:c)
for(i in c(1:c)) {
  pairsd[i]<-sd(pairsmatrix2[i,])}

detach("package:sna")

Result1<-data.frame(network="BIntraAgo",attribute="Group",
      metric="betweenness",random="nodeperm",teststat=H_obs,
      lowerp=lowerp,upperp=upperp,absp=absp, NaNomit=NAomit,
      testrandmean=randmean,testrandmedian=randmedian,testrandsd=randsd)

#Creating pairwise output file
observedpairs$pairpvalue<-pairpvalue
observedpairs$teststatmean<-pairmean
observedpairs$teststatmedian<-pairmedian
observedpairs$teststatsd<-pairsd
permmethod<-rep("nodeperm",times=c)
obsnetwork<-rep("BIntraAgo",times=c)
obsattribute<-rep("Group",times=c)
obsmetric<-rep("betweenness",times=c)
observedpairs_result1<-cbind(obsnetwork,obsattribute,obsmetric,
      permmethod,observedpairs)

####################################################################
#BIntraAgo vs Group with strength
####################################################################

#create grouping vector
metricvec<-attribute$BIntraAgo_strength

#Run permutations with node permutation
#calculate observed test stat
H_obs<-conover.test(metricvec,groupvec,method="by",table=FALSE)$chi2
obspairs<-conover.test(metricvec,groupvec,method="by",table=FALSE)$T
paircomp<-conover.test(metricvec,groupvec,method="by",
      table=FALSE)$comparisons
observedpairs<-data.frame(paircomp,obspairs)

#Create output matrix of pairwise comparisons
#c is number of pairs being compared as gathered from observedpairs file
c<-6
pairsmatrix<-matrix(0,nrow=c,ncol=P)
rownames(pairsmatrix)<-paircomp
random2<-rep(1:P)

#create sna matrix for randomization
```

```
library(sna)
snanet <- as.matrix(net)
N <- max(c(snanet[,"i"],snanet[,"j"]))
g <- matrix(data=0, nrow=N, ncol=N)
g[snanet[,c("i","j")]] <- snanet[,"w"]
snanet2<- as.sociomatrix.sna(g)

#Runn Conover-Iman's test for random networks

for (i in c(1:P)) {
  rand_df<-attribute[c("NumberID","ID")]
  node<-rand_df$NumberID
  rand_df<-cbind(rand_df,node)
  randnet<-rmperm(snanet2)
  metricrand<-degree_w(randnet, measure=c("degree","output","alpha"),
      alpha=0.5)
  metricrand2<-data.frame(metricrand)
  rand_df<-merge(rand_df,metricrand2,by="node",all=TRUE)
  rand_df[is.na(rand_df)]<-0
  Randmetricvec<-rand_df$output
  random2[i]<-conover.test(Randmetricvec,groupvec,method="by",
      table=FALSE)$chi2
  pairsmatrix[,i]<-conover.test(Randmetricvec,groupvec,method="by",
      table=FALSE)$T}

NAomit<-sum(is.nan(random2))
random3<-na.omit(random2)
pairsmatrix2<-t(na.omit(t(pairsmatrix)))
upperp<-sum(H_obs<random3)/P
lowerp<-sum(H_obs>random3)/P
absp<-sum(abs(H_obs)<abs(random3))/P
randmean<-mean(random3)
randmedian<-median(random3)
randsd<-sd(random3)

pairpvalue<-rep(1:c)
for(i in c(1:c)) {
  pairpvalue[i]<-sum(abs(obspairs[i])<abs(pairsmatrix2[i,]))/P}
pairmean<-rep(1:c)
for(i in c(1:c)) {
  pairmean[i]<-mean(pairsmatrix2[i,])}
pairmedian<-rep(1:c)
for(i in c(1:c)) {
  pairmedian[i]<-median(pairsmatrix2[i,])}
pairsd<-rep(1:c)
for(i in c(1:c)) {
  pairsd[i]<-sd(pairsmatrix2[i,])}

detach("package:sna")

Result2<-data.frame(network="BIntraAgo",attribute="Group",
      metric="strength",random="nodeperm",teststat=H_obs,lowerp=lowerp,
      upperp=upperp,absp=absp,NaNomit=NAomit,testrandmean=randmean,
      testrandmedian=randmedian,testrandsd=randsd)

#Creating pairwise output file
observedpairs$pairpvalue<-pairpvalue
observedpairs$teststatmean<-pairmean
observedpairs$teststatmedian<-pairmedian
observedpairs$teststatsd<-pairsd
permmethod<-rep("nodeperm",times=c)
obsnetwork<-rep("BIntraAgo",times=c)
obsattribute<-rep("Group",times=c)
obsmetric<-rep("strength",times=c)
observedpairs_result2<-cbind(obsnetwork,obsattribute,obsmetric,
      permmethod,observedpairs)
```

Appendix 3.VI: Checklists of which networks and metrics were dense enough for analysis of significant differences in metric values relative to attribute class.

Table 3.VI. 1. Checklist of adult takhi networks and metrics dense enough for analysis of significant differences in metric values relative to attribute class in Chapter 4. A √ indicates a network dense enough for inclusion in analysis, while a * indicates a network too sparse for analysis.

Season	Scale	Metric	Seer			Hustai		
			Spatial	Agonistic	Affiliative	Spatial	Agonistic	Affiliative
Non-breeding								
	Intra	Strength	√	√	√	√	√	√
		Degree	√	√	√	√	√	√
		Instrength	*	√	√	*	√	√
		Indegree	*	√	√	*	√	√
		Betweenness	√	√	*	√	√	*
		Clustering Coefficient	*	√	*	*	√	*
	Inter	Strength	√	√				
		Degree	√	√				
		Instrength	*	√				
		Indegree	*	√				
		Betweenness	√	√				
		Clustering Coefficient	√	√				
Breeding								
	Intra	Strength	√	√	√	√	√	√
		Degree	√	√	√	√	√	√
		Instrength	*	√	√	*	√	√
		Indegree	*	√	√	*	√	√
		Betweenness	*	√	*	*	√	√
		Clustering Coefficient	*	√	*	*	√	*
	Inter	Strength	√	√				
		Degree	√	√				
		Instrength	*	√				
		Indegree	*	√				
		Betweenness	√	√				
		Clustering Coefficient	√	*				

Table 3.VI. 2. Checklist of juvenile takhi networks and metrics dense enough for analysis of significant differences in metric values relative to attribute class in Chapter 5. A √ indicates a network dense enough for inclusion in analysis, while a * indicates a network too sparse for analysis.

Scale	**Metric**	**Seer**			**Hustai**		
		Spatial	Agonistic	Affiliative	Spatial	Agonistic	Affiliative
Intra	Strength	√	√	√	√	*	√
	Degree	√	√	√	√	*	√
	Instrength	*	√	√	*	*	√
	Indegree	*	√	√	*	*	√
	Betweenness	*	√	*	*	*	*
	Clustering Coefficient	*	√	√	*	*	√
Inter	Strength	√	√	√			
	Degree	√	√	√			
	Instrength	*	√	√			
	Indegree	*	√	√			
	Betweenness	*	√	*			
	Clustering Coefficient	√	√	√			

Table 3.VI. 3. Checklist of adult/juvenile takhi networks and metrics dense enough for analysis of significant differences in metric values relative to attribute class in Chapter 6. A √ indicates a network dense enough for inclusion in analysis, while a * indicates a network too sparse for analysis.

Season	**Scale**	**Metric**	**Seer**			**Hustai**		
			Spatial	Agonistic	Affiliative	Spatial	Agonistic	Affiliative
Non-breeding								
	Intra	Strength	√	√	√	√	√	√
		Degree	√	√	√	√	√	√
		Instrength	*	√	√	*	√	√
		Indegree	*	√	√	*	√	√
		Betweenness	√	√	√	√	*	*
		Clustering Coefficient	*	*	*	*	*	*
	Inter	Strength	√	√	√			
		Degree	√	√	√			
		Instrength	*	√	√			
		Indegree	*	√	√			
		Betweenness	√	√	*			
		Clustering Coefficient	*	*	*			
Breeding								
	Intra	Strength	√	√	√	√	√	√
		Degree	√	√	√	√	√	√
		Instrength	*	√	√	√	√	√
		Indegree	*	√	√	√	√	√
		Betweenness	√	√	*	√	√	√
		Clustering Coefficient	*	*	*	*	*	*
	Inter	Strength	√	√	*			
		Degree	√	√	*			
		Instrength	*	√	*			
		Indegree	*	√	*			
		Betweenness	√	√	*			
		Clustering Coefficient	*	*	*			

Appendix 5.I: Example of RStudio code used to test for a significant difference in network metrics (betweenness, strength, degree, instrength, indegree, and clustering coefficient) relative to sex for juveniles at Seer and Hustai using a Wilcoxon-Mann-Whitney U test. This example shows the code for comparing betweenness and weighted degree scores in the juvenile intragroup spatial network at Seer among individuals of differing sex for analyses presented in Chapter 5. To apply the code to different networks, input and output file names were changed depending on the season, location, and age group for which metrics were being compared. Any line of code preceded by '#' indicates instructions or description, rather than actual code.

```
######################################
##Juvenile Network Difference By Sex##
######################################

library(tnet)
P<-5000
NetworkInput<-JuvIntra
net<-as.tnet(NetworkInput, type="weighted one-mode tnet")
##if distance, symmetrise network##
net<-symmetrise_w(net,method="SUM")

attribute<-JuvenileAttributeMetrics

###############
##Betweenness##
###############

#Calculate observed statistic#
male<-attribute[which(attribute$Sex=="M"),]
female<-attribute[which(attribute$Sex=="F"),]
U_obs<-wilcox.test(male$JuvIntra_between,female$JuvIntra_between,
paired=FALSE)$statistic

#Create random networks
U_rand<-rep(0,P)

for (i in c(1:P)) {
  rand_df<-attribute[c("NumberID","ID","Sex")]
  node<-rand_df$NumberID
  rand_df<-cbind(rand_df,node)
  randnet<-rg_reshuffling_w(net,option="weights")
  metricrand<-betweenness_w(randnet, alpha=1.5)
  metricrand2<-data.frame(metricrand)
  rand_df<-merge(rand_df,metricrand2,by="node",all=TRUE)
  rand_df[is.na(rand_df)]<-0
  male_rand<-rand_df[which(rand_df$Sex=="M"),]
  female_rand<-rand_df[which(rand_df$Sex=="F"),]
  U_rand[i]<-wilcox.test(male_rand$bet,female_rand$bet,
      pair=FALSE)$statistic}

NAomit<-sum(is.nan(U_rand))
U_rand2<-na.omit(U_rand)

upperp<-sum(U_obs<U_rand2)/P
lowerp<-sum(U_obs>U_rand2)/P
absp<-sum(abs(U_obs)<abs(U_rand2))/P
randmean<-mean(U_rand2)
randmedian<-median(U_rand2)
randsd<-sd(U_rand2)
```

```
Result1<-data.frame(network="JuvIntraDist",attribute="Sex",
      metric="betweenness",random="weights",teststat=U_obs,
      lowerp=lowerp,upperp=upperp,absp=absp, NaNomit=NAomit,
      testrandmean=randmean,testrandmedian=randmedian,testrandsd=randsd)

##########
##Degree##
##########
#Calculate observed statistic#
male<-attribute[which(attribute$Sex=="M"),]
female<-attribute[which(attribute$Sex=="F"),]
U_obs<-wilcox.test(male$JuvIntra_degreeA0.5,female$JuvIntra_degreeA0.5,
      paired=FALSE)$statistic

#Create random networks
U_rand<-rep(0,P)

for (i in c(1:P)) {
  rand_df<-attribute[c("NumberID","ID","Sex")]
  node<-rand_df$NumberID
  rand_df<-cbind(rand_df,node)
  randnet<-rg_reshuffling_w(net,option="weights")
  metricrand<-degree_w(randnet, measure=c("degree","output","alpha"),
      alpha=0.5)
  metricrand2<-data.frame(metricrand)
  rand_df<-merge(rand_df,metricrand2,by="node",all=TRUE)
  rand_df[is.na(rand_df)]<-0
  male_rand<-rand_df[which(rand_df$Sex=="M"),]
  female_rand<-rand_df[which(rand_df$Sex=="F"),]
  U_rand[i]<-wilcox.test(male_rand$alpha,female_rand$alpha,
      pair=FALSE)$statistic}

NAomit<-sum(is.nan(U_rand))
U_rand2<-na.omit(U_rand)

upperp<-sum(U_obs<U_rand2)/P
lowerp<-sum(U_obs>U_rand2)/P
absp<-sum(abs(U_obs)<abs(U_rand2))/P
randmean<-mean(U_rand2)
randmedian<-median(U_rand2)
randsd<-sd(U_rand2)

Result3<-data.frame(network="JuvIntraDist",attribute="Sex",
      metric="degreeA0.5",random="weights",teststat=U_obs,lowerp=lowerp,
      upperp=upperp,absp=absp,NaNomit=NAomit,testrandmean=randmean,
      testrandmedian=randmedian,testrandsd=randsd)
```