Social stability in semiferal ponies: networks show interannual stability alongside seasonal flexibility

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Long-term relationships that underlie many stable mammalian groups often occur between philopatric kin. Although stable groups of nonrelatives appear to be less common, there is increasing evidence that social bonds between nonkin may confer sufficient intrinsic fitness benefits for these groups to persist. Here we evaluate whether social stability occurs in a bisexually dispersing species where social bonds have been shown to have reproductive benefits: the feral horse, *Equus caballus*. First, we quantified female social stability by applying a three-level framework to a 3-year data set of associations in semiferal ponies; this tested for stability at the individual, dyadic and subpopulation levels. Despite the relative weakness of these female bonds, we found significant social stability across all levels, as shown by stable association preferences, social networks and individual network positions. Second, we investigated how seasonality impacts on social bond strength and grouping patterns. We found seasonal fluctuations in female gregariousness, with a peak during the mating season. We therefore propose that significant social stability in female horses is coupled with a degree of flexibility that allows for effects of ecological fluctuations. Although social network analysis is widely used in behavioural ecological research, this is one of only a handful of studies to assess the temporal dynamics of networks over a significant timescale. Temporal stability in female relationships suggests that equid social structures are multifaceted: although bonds between stallions and mares are clearly strong, long-term relationships between mares underpin the social network structure. We suggest this framework could be used to assess social stability in other group-living species in order to improve our understanding of the nature of social bonds.

In mammals, female philopatry can lead to stable kin-based groups (Archie et al., 2006; Holekamp et al., 1997; Kerth & van Schaik, 2012); delayed dispersal is thought to provide indirect fitness benefits by promoting cooperation with kin (Hatchwell, 2010). Such relationships between kin may have evolved as a result of the persistence and generalization of mother–offspring bonds beyond the time of nutritional dependence (Curley & Keverne, 2005), which then expanded to include bonds among kin for purposes such as allomothering in African elephants, *Loxodonta africana (Lee, 1987)*. Stable groups of nonrelatives are less commonly reported; nonkin groups are more frequently depicted as aggregations of individuals that share common requirements (e.g. Fischoff, 2009). In these social structures, group composition can vary as individual needs change with seasons or physical requirements (e.g. sexual segregation patterns in ungulates; Ruckstuhl & Neuhaus, 2000, 2002). Stable nonkin groups, however, have been described in birds and are thought to be the consequence of the benefits of cooperative rearing (e.g. eider ducks, *Somateria mollissima*: Ost et al., 2005) or in insects where cooperation between nonkin may be due to the direct benefits of increased group size (Costa & Ross, 2003).

Stable groups, comprising either kin or nonkin, require coordination and collective decision making to maintain cohesion and are unlikely to persist unless benefits are significant. Compromise is required to coordinate a group's activities (Conradt & Roper, 2005; Dunbar & Shultz, 2010). Sufficient time must also be allowed for appropriate servicing of the social bonds that maintain these groups (e.g. grooming: Dunbar, 1991; Hart & Hart, 1992). Since time budgets are constrained by a number of essential activities such as obtaining food, there is an inherent limit to the number of relationships that can be adequately maintained in the time left over to social activities (Lehmann et al., 2007). The feasibility of maintaining stable groups is particularly difficult where the abundance of food

varies seasonally, resulting in fluctuating bond strength (Foster et al., 2012; Henzi et al., 2009; Holekamp et al., 2012). Social stability, although fairly common among anthropoid primates (Shultz & Dunbar, 2007), is less common among other mammals.

In addition to group-level benefits, such as reducing predation risk, strong social bonds within groups may confer additional benefits (Dunbar, 1998). For example, in kin groups of wild savannah baboons, *Papio cynocephalus*, more socially integrated adult females have higher rates of infant survival (Silk et al., 2003) and more sociable bottlenose dolphin, *Tursiops truncatus*, females have a higher calving success (Frere et al., 2010). Importantly, recent work has highlighted that clear fitness benefits are obtained by animals that form groups of nonkin, suggesting that the drive to form a long-term bond may itself be a major driver for an individual to join, or remain in, a group (Seyfarth & Cheney, 2012). For example, dispersing male Assamese macaques, *Macaca assamensis*, gain clear fitness benefits from forming strong bonds since males engaging in coalitions have higher future dominance levels and therefore reproductive success (Schuelke et al., 2010). Increased fitness has also been demonstrated in more socially integrated female horses, *Equus caballus*, which have higher reproductive success in terms of both foaling rate and offspring survival (Cameron et al., 2009). These females are assumed to be nonrelatives due to the prevalence of bisexual dispersal in this species (Boyd & Keiper, 2005). In addition, researchers have recently demonstrated that the number of associates has a significant effect on foal survival following a catastrophic event (Nunez et al., 2015), further evidence for direct benefits of social bonds in horses. Given the fitness benefits of social integration, we therefore chose to evaluate the temporal social stability of relationships within groups in semiferal ponies where kin structure does not underpin social groups.

Free-living horses live in harem groups (bands) normally consisting of one or two

males, a small number of females and their predispersal offspring (Rubenstein & Wrangham, 1986). Upon dispersal around the age of 2 years, females can join other existing bands or form new bands with bachelor males; males either join bachelor groups or form their own band if they can recruit females directly (Boyd & Keiper, 2005). Despite short-term fission–fusion, band composition remains relatively stable over time (Scorolli & Lopez Cazorla, 2010). Although strong stallion–mare bonds are thought to underpin group structure (Linklater, 1999), females can remain as a group after the death of their stallion (Klingel, 1982; Rubenstein, 1994). Feral horse populations also occupy a wide range of habitats (Boyd & Keiper, 2005), yet apparently all retain stable harems despite highly varied ecological pressures (Linklater, 2000), suggesting an ecologically independent benefit of social stability. Horses are, therefore, an ideal model system in which to explore drivers of social stability as, in contrast to many of the Old World primate species in which stable relationships have been demonstrated (e.g. chacma baboons, *Papio ursinus*: Silk et al., 2012), dispersal by both sexes means that individuals in a social group are unlikely to be closely related (Cameron et al., 2009).

Our major aim in this study was to quantify social stability in bonds between female horses and to investigate seasonal effects upon bond strength. We used social network analysis, a technique which although commonly used to describe social structure (Farine & Whitehead, 2015; Pinter-Wollman et al., 2014) has only rarely been used to assess temporal dynamics of social relationships (e.g. Henzi et al., 2009; Hobson et al., 2013, see Pinter-Wollman et al., 2014, for a review of this field). Longitudinal studies, particularly those that measure social stability or the responses of social networks to ecological perturbations, are rare (Pinter-Wollman et al., 2014; Sih et al., 2009; Wey et al., 2008). Most studies capture a single window of animal social relationships; however, the choice of timescale the snapshot

represents can have a major influence on results (Cantor et al., 2012; Flack, 2012). Relative stability of relationships within a given time frame is often assumed (Wey et al., 2008), yet few studies have considered how temporal changes can shed light on the dynamics of social networks (Pinter-Wollman et al., 2014). Stability can be assessed at three levels: for the individual, for dyadic relationships and at the population level. In an unchanging network we would assume that stability is manifest in all three. However, changes in individual position or in preferred relationships may have little impact on the overall network, and vice versa. We hope to address these issues by presenting a novel analytical framework, assessing stability at each of these three levels. A similar approach has been used to assess short-term temporal dynamics of networks of newly formed groups (Hobson et al., 2013), but this paper is, to our knowledge, the first to assess social stability across a longer time frame.

To quantify social stability in horses, we collected data on associations within a large population of semiferal ponies in the Carneddau Mountains, North Wales, U.K., between 2009 and 2012. We first evaluated the relative importance of season, year and relationship types (e.g. mother–offspring, female–male) on the strength of dyadic bonds in horses. We expected bonds between close kin (e.g. mother–offspring) to be stronger than those between nonkin (e.g. female–female) and that season would affect gregariousness due to changes in levels of stallion harassment and food availability. We then tested for seasonal effects on average female gregariousness and quantified seasonal fluctuations in population-level female association networks. Since stable associations may be a response to male harassment (Linklater et al., 1999), we predicted that social bond strength would be highest in the mating season, when food availability is also at a high level. We finally tested for long-term social stability by implementing a novel analytical framework. This tests for stability at three distinct levels: at the individual level, in terms of stability in network positions (i.e. how

central individuals are within the network); at the dyadic level, in terms of the stability in ranked dyadic bond strength; and at the population level, in terms of stability in the overall female social network. For female horses to show a high degree of social stability, as we would expect from field observations and current understanding of horse behavioural ecology (Boyd & Keiper, 2005), we predicted that all these criteria would be met.

METHODS

Study Population

We conducted this study in the Carneddau Mountain range, North Wales (53.22°N, 3.95°W), U.K. between February 2009 and February 2012, with observations made during all seasons. The study site is mountainous terrain ranging in altitude from 250–950 m (see Stanley & Shultz, 2012, for details). The study population consisted of around 200–300 semiferal Carneddau-type Welsh mountain ponies, which range freely across an area of approximately 200 km^2. Eighty-three individuals from three focal bands (defined as associations of mares, their predispersal offspring and one or more stallions who defend the group; Linklater, 2000) were observed for approximately 3 days per month; the three focal bands were named 'Aber', 'Anafon' and 'Marsh'. Individuals were photographed and identified by distinctive markings, coat colour and ear notches. The population experiences no anthropogenic interference apart from an annual round-up in November when some young males are removed from the mountains; no focal individuals were removed during this observation period and no data were collected for 2 weeks following the round-up, to allow for bands to re-establish themselves.

Field Observations

A total of 240 h of observations were carried out over 81 days (by C.S.); this allowed a mean ⬚ SE total of 108.3⬚3.95 scans per individual. To ensure unbiased sampling, an area of approximately 30 km^2, comprising the major proportion of the home ranges of three focal bands, was traversed on foot each day. Whenever a subgroup (see later definition) was encountered, a single group scan was carried out to record the total number of individuals present, their identities and to map their spatial distribution by recording intradyadic distances (IDD), the distances between neighbouring individuals, in metres. IDDs were estimated to the nearest 5 m by eye and recorded on sketch maps. Scans were repeated at 30 min intervals to a maximum total of four scans, unless a subgroup split up or went out of sight. If the subgroup split up, one group was followed at random and further scans carried out until the maximum of four scans had been reached. A minimum of two scans was carried out per subgroup and it was sometimes possible to observe more than one group from one location. Individuals were deemed to be members of the same subgroup when they were within 200 m of at least one other individual (we defined the cutoff distance as >95% of observations) and maintained this level of proximity or less over the sampling period; if individuals moved away from the group or were left behind following the group's movement, they were not included in subsequent scans. Data were collected over a 5–6 h period between 0900 and 1700 hours (with data collection finishing at 1600 hours in winter months due to lack of daylight), with sampling effort remaining relatively constant throughout the year (although winter access was sometimes restricted due to snow) to obtain unbiased estimates of association patterns (Henzi et al., 2009). Sampling effort was

targeted at all bands equally.

Data Analysis

First, a weighted IDD (wIDD) value was calculated for each dyad for each scan to create an association index varying between zero (no association) and one (highest level of association). The minimum IDD was set at 15 m (i.e. for any dyads that were less than 15 m apart, a value of 15 was assigned) in order to minimize error incurred while estimating smaller intradyadic distances; dyads were often at a considerable distance from the researcher, meaning the accuracy of distance estimates may not be sufficiently reliable below this value. A weighted IDD (wIDD) value was then calculated for every scan for every potential dyad by dividing 15 by the observed IDD value (i.e. by calculating the inverse), or by assigning a value of zero if two animals were not in the same subgroup during this scan. This meant that two individuals within a 15 m radius were assigned a value of 1, individuals that were more than 15 m apart were assigned a value between 0 and 1 (scaled by distance) and any two animals that were not in the same subgroup, including all those in other bands, were assigned a value of 0. Thus, every possible pairing of individuals was assigned an IDD value for each sampling point. A mean wIDD was then calculated for each possible dyad for each season, with these values being used to produce a symmetrical proximity matrix. This method of averaging data over a specific time block (a season in this case) is recommended by Farine and Whitehead (2015) to overcome the issue of nonindependence of sequential observations.

Seasonal and annual effects on social proximity

We defined relationship classes by the age and sex of each member of the dyad: subadults were predispersal individuals under 3 years old of either sex, while females and males were sexually mature adults. Foals were excluded from this data set due to their presumed dependence upon their mother. The relationship classes therefore categorized dyads as either male–female, female–female, female–subadult offspring (where suckling had been observed), female–subadult nonoffspring, male–offspring (where all subadults in a band were assumed to be the harem male's offspring) or subadult–subadult.

We fitted a linear mixed-effects (LME) model (using the 'lme' function in the package nlme; Pinheiro et al., 2013, in R 3.0.0, R Development Core Team, 2013) with wIDD between all possible dyads within each band as the dependent variable and year, season, relationship class and all second-order interactions as fixed factors, and a nested random factor comprising the identities and band membership of the dyad members. Eighty-three individuals were represented in the model, of which 29 were adult females, 5 were adult males and 49 were subadults. To correct skew, we square-root transformed the wIDD data prior to fitting the model. We tested the resulting model fit by examining a density plot of the residuals, a residual-fitted value plot and a Q–Q plot. Box plots were then drawn to show effect sizes for factors with a significant effect on wIDD.

To determine whether season had a significant effect on average subgroup size, we also square-root transformed subgroup size data and fitted a glm in R, using the glht command in the package multcomp (Hothorn et al., 2008) for post hoc pairwise comparisons. We evaluated model fit as above.

Seasonal and annual effects on social network metrics

We built annual and seasonal proximity networks for adult females only from all

bands combined using wIDD scores. Matrices were built for each season (defined as mating (April–June), raising young (July–September) and winter (October–March), as these blocks incorporated both seasonal food availability and breeding events) and for each year, thus generating nine seasonal and three annual proximity matrices.

We used proximity as a measure of bond strength here since behavioural interactions such as mutual grooming, which are often used in other studies to quantify the strength of social bonds (e.g. Wey & Blumstein, 2010), were too infrequently observed in these ponies to allow reliable networks to be built for all seasons. However, we also collected data on affiliative and aggressive interactions using all-occurrence sampling (Altmann, 1974) in between scan samples and correlated the networks built using these data for one band (only Aber band showed sufficient behavioural interactions recorded for networks to be built using these data) with proximity networks (Appendix). Since the affiliative network (and one based on subgroup membership) significantly correlated with the proximity network (affiliation versus proximity quadratic assignment procedure (QAP) test: $r = 0.544$, $P < 0.01$; subgroup versus proximity QAP test: $r = 0.935$, $P < 0.001$; see below for QAP test details), but there was no significant correlation between the aggression and proximity networks (aggression versus proximity QAP test: $r = 0.200$, $P = 0.195$; Appendix), we can justify the use of proximity networks as a reliable proxy for affiliative relationships in ponies.

First, we used QAP correlation tests between each possible pairing of the nine seasonal proximity matrices in order to (1) examine stability across seasons and (2) quantify fluctuations in correlation strength between seasons as recommended by Hobson et al. *(2013)*. The QAP correlation test is a specialized version of the Mantel test, which carries out random permutations of node labelling from the observed matrix to determine whether correlations between two specified matrices are significantly higher than expected (Butts,

2010; Croft et al., 2011; Krackhardt, 1988; Wey & Blumstein, 2010). It has been previously used to assess correlations between matrices built for the same individuals using different association indices (Wey & Blumstein, 2010) and to evaluate stabilization patterns of social structure in newly formed groups (Hobson et al., 2013). QAP correlation tests were carried out with 10 000 permutations in the package statnet (Handcock et al., 2003) in R 3.0.0 with Bonferroni corrections applied to correct for multiple testing (Dunn, 1961). We also calculated the estimated magnitudes of matrix correlations and their associated 95% confidence intervals to indicate the level of social stability across seasons using the package psychometric (Fletcher, 2013) in R 3.0.0, with the sample size taken to be the total number of vertices across both networks.

Second, in order to quantify the effect of season on the levels of general female gregariousness, we used the package tnet *(Opsahl, 2009)* in R 3.0.0 to calculate an individual female's strength centrality within each of the nine seasonal proximity networks. Strength centrality quantifies female gregariousness as it takes into account both the number of immediate bonds and their individual weights (Croft et al., 2008) and is calculated by the formula:

$s_i = \sum_{j=1}^{n} W_{ij}$ where S_i is the strength centrality for individual *i*, W_{ij} is the weight of tie between individuals *i* and *j*, and *n* is the number of individuals in the network.

We then explored temporal patterns in these mean strength centrality measures by fitting an LME model with strength centrality as the dependent variable (no transformation required), season and year as fixed factors, and individual ID as a random factor. Box plots were produced to visualize results.

Assessment of social stability

We then applied a novel framework to assess levels of social stability comprising three distinct stages. First, we tested for stability in relative female bond strength (dyadic level). Female dyads were ranked within each year according to their mean wIDD values across the entire year (taken from annual proximity matrices). To test for a correlation among mean wIDD ranks over the 3 years within dyads, we calculated an intraclass correlation coefficient (ICC; Bartko, 1966) using the package irr (Gamer, 2010) in R 3.0.0. Ranking was used so that stability in relative, not absolute, bond strength could be assessed as seasonal/annual effects on absolute bond strength were investigated in a previous section. Second, we examined stability in the annual female proximity networks (population level) by using pairwise QAP correlation tests, again reporting the magnitude of the correlations and their associated 95% confidence intervals. Third, we tested for stability in female annual network positions using strength centrality (the sum of tie weights to all adjacent nodes; Croft et al., 2008) and closeness centrality (the inverse of the sum of the distances to all nodes in the network; Wasserman & Faust, 1994). Both measure how well connected an individual is in a network in slightly different ways; while strength centrality considers the number and weighting of immediate connections to neighbouring nodes, closeness centrality also incorporates indirect ties to all members of a network. These were calculated using the R package tnet. We then ranked each individual in terms of strength/closeness for each year separately, using the ICC (as above but with individuals, not dyads, being assigned a rank) to test for a significant correlation in ranks over the 3 years. Annual networks were visualized using NetDraw (Borgatti, 2002).

Ethical Note

Permission to carry out this study was given by Snowdonia National Parks, the National Trust and the Carneddau Pony Society. These ponies are habituated to the presence of humans as the area is frequented by hill walkers; this research therefore caused minimal disturbance. Behavioural observations were carried out from a minimum of 30 m from the focal individuals, a distance at which walkers frequently pass the ponies. At the time of the study, noninvasive animal studies did not require university ethics clearance.

RESULTS

Factors Affecting Social Bond Strength

All main effects and second-order interactions were significantly associated with our proximity measure, wIDD (Table 1, Fig. 1). The closest dyadic proximity was maintained in the mating season (Fig. 1a); annual effects on variation in wIDD were also apparent. Mothers and their subadult offspring maintained closer proximity than other bond classes (Fig. 1b).

Seasonal Effects

The nine seasonal female proximity networks all showed significant interseasonal stability, as indicated by $P < 0.01$ for all QAP tests between pairs of consecutive seasons (remaining significant following a Bonferroni correction). However, the magnitude of these correlations did show some variation; while there was no clear pattern to these changes, the correlation strength fluctuated between 0.5 and 0.85 between pairs of seasons (Fig. 2). We

found that mating season was associated with the highest strength centrality of these females ($F_{2,182}$ = 23.83, P < 0.001; mating season*raising young: 0.63 ± 0.11, t_{182} = -5.69, P < 0.001; mating*winter: 0.68 ± 0.11, t_{182} = -6.23, P < 0.001); there was no effect of year on strength centrality (Fig. 3).

We also found a significant effect of season on mean ± SE female subgroup size (mating: 9.34 ± 0.36; raising young: 7.83 ± 0.35; winter: 7.22 ± 0.38; $F_{3,703}$ = 9.80, P < 0.001). Post hoc comparisons showed subgroup size to be significantly higher during the mating season than during raising of young (β ± SE = 0.26 ± 0.09, N_1 = 273, N_2 = 238, Z = 2.99, P = 0.008) or the winter (β ± SE = 0.38 ± 0.09, N_1 = 273, N_2 = 195, Z = 4.25, P < 0.001) seasons. There was no significant difference between raising young and winter seasons (β ± SE = 0.13 ± 0.09, N_1 = 238, N_2 = 195, Z = 1.37 P = 0.35).

Assessment of Social Stability

Significant social stability in female associations was evident for each of the three measures used. First, ranked female bond strength (measured by weighted IDD) significantly correlated across the 3-year period for all dyads combined (ICC = 0.21, $F_{67,136}$ = 1.80, P < 0.01), thus indicating consistency in association preferences. Second, annual female proximity networks (Fig. 4) showed significant stability across the 3-year period, as indicated by significant correlations for each of the pairwise QAP tests carried out (2009–2010: r = 0.598 (95% CI 0.528,0.660), P < 0.001; 2009-2011; r = 0.459 (95% CI 0.375,0.535), P < 0.001; 2010-2011; r = 0.685 (95% CI 0.628,0.734), P < 0.001: all P values remained significant following a Bonferroni correction). Third, female network positions remained significantly stable in terms of their centrality rankings for both centrality measures over the 3-year

period (strength centrality: ICC = 0.304, $F_{22,46}$ = 2.31, $P < 0.01$; closeness centrality: ICC = 0.573, $F_{22,46}$ = 5.03, $P < 0.001$).

DISCUSSION

Here, we show for the first time that stable social bonds occur between female horses, with evidence of stability present in multiple measures of social organization. These result in socially stable groups of unrelated individuals persisting over a number of years, with individual females retaining stable network positions. Such stability occurs despite seasonal fluctuations in female gregariousness, implying a level of flexibility in the network structure. This study demonstrates that social stability can evolve in the absence of high female–female kinship levels, where social bonds must nevertheless confer significant benefits, and implies a relatively high degree of social complexity in horses. Long-lived social bonds between nonrelative mammals have previously been demonstrated only in some Old World primates (e.g. chimpanzees, *Pan troglodytes*: Mitani et al., 2000) and in humans (Hill et al., 2011). We also found both closer sustained proximity between females and larger subgroup sizes in the mating season. Although these results could be explained by increased herding of females by the harem stallion during this season, active herding by the focal stallions was not frequently observed; increased female sociality in the mating season may therefore occur due to the reproductive benefits that are thought to derive from a reduction in male harassment (Cameron et al., 2009). While female–female bonds are relatively weak compared to kin-based mother–offspring bonds, they are likely to be longer lasting and therefore important in maintaining band cohesion.

The novel framework we applied here to test for social stability evaluates multiple measures of relationships and provides a significant advance in the methods used to quantify temporal network dynamics. We used three measures to test for social stability in horses: stability in relative bond strength, stability in proximity networks and stability in individual network positions over a 3-year period. These form a simple framework for the assessment of social stability in other species, as well as providing a benchmark of social complexity in this species. The three measures quantify different levels of social stability: at the individual level, we showed that network positions in terms of both strength and closeness centrality were consistent; at the dyadic level, we demonstrated that female horses show stability in their association choices (i.e. the ranked strength of dyadic bonds was consistent); and at the subpopulation level, the proximity network comprising three social groups showed significant stability. It may be that in other species not all these premises can be met; this framework could therefore be used to compare relative levels of social stability across species. Stable groups appear to be uncommon outside of anthropoid primates (Shultz & Dunbar, 2007); this study's verification of social stability in female horses allows for the possibility of higher levels of cooperation in this species, such as cultural information transfer (Hoppitt & Laland, 2008) and societal roles such as policing (Flack et al., 2005), which are restricted to species with sufficient social complexity to allow for their evolution.

Stable female relationships in groups of horses are not underpinned by high kinship levels. Although stable relationships have been previously documented in a number of mammal species, most are between close kin (e.g. chacma baboons: *Silk et al., 2012*; Indo-Pacific bottlenose dolphins, *Tursiops aduncus*: *Wiszniewski et al., 2010*; giraffes, *Giraffa camelopardalis*: Bercovitch & Berry, 2013; Carter et al., 2013), although long-term

relationships have been demonstrated between dispersed female chimpanzees (Lehmann & Boesch, 2009). Male harassment is known to reduce reproductive success in female horses (Cameron et al., 2009; Linklater et al., 1999; Rubenstein, 1994; Rubenstein & Wrangham, 1986); increased sociality is thus thought to result in increased female fitness (Cameron et al., 2009). We therefore provide further evidence that social bonds themselves must be sufficiently beneficial to overcome the costs associated with their maintenance since they are stable across a significant period of time in this population.

Seasonal fluctuations were evident in the magnitude of correlation strengths between female proximity networks (built using wIDD; Fig. 2), despite long-term network stability. Female subgroup sizes were also significantly larger in the mating season than in other seasons, with females showing higher strength centrality in this season (Fig. 3). While grass productivity may be higher in this season, horses do not defend patches, as food is relatively evenly distributed over a wide area (Boyd & Keiper, 2005). Therefore, a social explanation for female gregariousness patterns is more likely than those relating to seasonal food abundance. Male harassment is known to reduce reproductive success in female horses (Cameron et al., 2009; Linklater et al., 1999); this is expected to be higher in the mating season, when females come into oestrus (McDonnell, 2005). It is therefore likely that females are more proximate during the mating season as this reduces levels of male harassment experienced via a dilution effect. Male herding behaviour alone is unlikely to explain this increased proximity between females; in another study, incidences of females rejoining bands were rarely associated with male herding (Kaseda & Khalil, 1996). Gregariousness has also been linked to the oestrous cycle in female chimpanzees; party size has been shown to increase when more females are in oestrus (Wittiger & Boesch, 2013). Our results are therefore consistent with the idea that increased female gregariousness in

horses is as a direct response to male harassment (Linklater et al., 1999). Therefore, in addition to social bonds between mares and their band stallion, the stability of female within-group relationships indicates another layer of organization. Thus, even where stallions would prefer additional females to join their bands, successful female integration into groups is likely to be at least partially determined by their ability to form relationships with resident females (Rubenstein & Nunez, 2009).

We also found annual variation in the mean magnitude of social bond strength (as measured by wIDD); this may reflect population-scale social network changes, due to social factors such as changes in interband spacing behaviour (Linklater, 2000), or ecological factors such as changes in local food availability (Foster et al., 2012; Henzi et al., 2009; Holekamp et al., 2012). Bond strength varied between relationship classes due to differences in both the function and duration of these bonds. As predicted, bonds between mothers and offspring, those sharing the highest level of kinship in a horse band, were the strongest (Fig. 1b). However, it is important to remember these are unlikely to contribute to band stability as juveniles generally disperse at 2–3 years of age (Boyd & Keiper, 2005); these bonds are therefore much more short-lived than the band itself. It is commonly believed that it is the male–female bond that maintains cohesion in horse groups as males attempt to defend harems of females from other males (Boyd & Keiper, 2005). However, our results indicate that the strength of bonds between mares and stallions does not differ greatly from other bond classes (Fig. 1b); female–female bonds may therefore be equally important for group cohesion. Since the same three males retained harem tenure for the focal bands in this study from start to finish of the data collection period, we are unable to investigate the effects that stallion turnover may have on female bond stability from this data set; stallion turnover events do tend to reduce band stability (Boyd & Keiper, 2005). However, females

have also been observed to remain as a group following the death of the band stallion (Klingel, 1982; Rubenstein, 1994). Future studies could investigate the persistence of female bonds during times of band instability in order to better ascertain their benefits. What our study does show is stability within group relationships; this is noteworthy as stable group composition does not necessarily lead to stable social relationships within the group. Moreover, stable group composition will not necessarily lead to stable network structure, particularly where networks within groups are not fully connected.

This study provides further insights into the temporal dynamics and structure of animal social networks. First, we have shown that social stability can occur over a longer time frame, but that bond strength can fluctuate seasonally within this stable framework; this implies that animal networks must be sufficiently flexible to accommodate these changes. Second, weaker bonds such as those between female horses may be overlooked as they are not as immediately obvious as, for example, mother–offspring bonds. However, in the case of horses, juveniles disperse yet females may stay together for life (Klingel, 1982), so these weaker female bonds are most likely to be driving horse social structure. Weaker ties may allow a social group increased flexibility to exploit more widespread resources (Maryanski, 1987) and so may explain why horses are able to persist across such a wide ecological range (Linklater, 2000). Third, we have demonstrated the merits of a long-term data set in exploring animal networks. Social stability can be demonstrated when periods spanning several years are considered; if shorter timescales are used, cyclical seasonal fluctuations in bond strength could lead to false conclusions that bonds are not enduring. Therefore, care should be taken to match the timescale selected to the question being asked in behavioural studies.

Acknowledgments

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Appendix

Measures of Bond Strength

Of the many indices of strength of social bonds, no one measure has proven consistently applicable and relevant (Dunbar & Shultz, 2010). We therefore calculated two additional behavioural indices and one measure of the consistency of subgroup membership that were then compared to justify the use of proximity as a measure of bond strength in horses for the major analyses.

Social behaviour between females was recorded on an all-occurrence basis (Altmann, 1974) as the entire group could always be observed. We recorded all aggressive interactions, defined as those where one animal's behaviour caused the displacement of another or involved biting, kicking or threats (Vervaecke et al., 2007), and all affiliative contact, defined as interactions where one individual approached another to touch, groom or sniff without any displacement or aggression occurring. Exceptions to this were sexual interactions (where a male approached a female and either attempted to mount her or exhibited flehmen behaviour) and suckling.

Two female behavioural networks were built for each band: 'affiliative contact' and 'aggression'. Dyads were linked if they had been recorded engaging in these behaviours at any point over the 3-year study period; it was necessary to collapse data over 3 years to build meaningful networks as both affiliative contact and aggression between adults were relatively infrequent. Affiliative contact and aggression networks built for Anafon and Marsh bands were discarded due to a paucity of data points. These networks were binary and therefore proximity networks had to be dichotomized prior to any comparison. To do this,

we kept the number of ties (*x*) constant in both networks; the *x* dyads with the lowest wIDD values (i.e. the most proximate) in the proximity network were assigned a value of 1, with all others being assigned a value of 0. The two binary networks (e.g. proximity and affiliation) could then be correlated using a QAP test.

The simple ratio index (SRI; Ginsberg & Young, 1992) was also calculated as a measure of the consistency of co-membership of a subgroup for a particular dyad. This index is appropriate where the likelihood of identifying a dyad is independent of whether or not two individuals are currently associated (i.e. where both individuals are consistently correctly identified either alone or in a pair: Cairns & Schwager, 1987) and is preferable to other estimators as it is statistically unbiased (Ginsberg & Young, 1992). A subgroup membership network was built using this measure as a direct weighting for network ties since it ranges between 0 and 1; a tie of 1 corresponds to two individuals always being in the same subgroup, with decreasing values indicating less frequent subgroup co-membership. This was then compared to the weighted proximity network using a QAP test.

Aber's female affiliative contact network was positively correlated with its corresponding binary proximity network (QAP test: $r = 0.544$, $P < 0.01$). No correlation was evident between the proximity and aggression networks (QAP test: $r = 2.000$, $P = 0.195$). The subgroup membership network significantly correlated with the proximity network for all bands combined (QAP test: $r = 0.935$, $P < 0.001$). These results therefore justify the use of proximity as a measure of bond strength; female dyads are more proximate and also engage in more affiliative behaviour without a corresponding increase in aggression, such as is found in more loosely bonded species such as goats (Stanley & Dunbar, 2013). Females also spend a larger proportion of time in the same subgroup, therefore choosing to stay together despite possible conflicting nutritional demands.

Table 1

Results of a linear mixed-effects model to estimate the relative effects of different factors upon weighted interdyadic distances (wIDD) between band members

Factor	*ndf*	*ddf*	*F*	*P*
(Intercept)	1	1459	958.47	<0.0001
Class	5	1459	14.06	<0.0001
Year	2	1459	10.62	<0.0001
Season	2	1459	31.06	<0.0001
Season:Class	10	1459	3.00	0.0009
Season:Year	4	1459	6.22	<0.0001
Class:Year	10	1459	1.99	0.0310

Numerator and denominator degrees of freedom (*ndf*, *ddf*) are given. IDs and band were incorporated as a nested random effect. 'Class' represents relationship class (e.g. female–female or mother–subadult offspring). The F statistics reported are from a marginal anova from the lme.

Figure 1. Pony proximity measures (inverse of weighted interdyadic distance (wIDD), square-root transformed) displayed as (a) year by season and (b) age–sex class by season. Seasons: mating: April–June; raising young: July–September; winter: October–March. Age–sex class combinations of dyads: SA = subadult; OS = offspring subadults; St = stallion. The boxes are bounded by the upper and lower quartiles and divided by the median. Maximum and minimum values within 1.5 box lengths of the quartiles are represented by the ends of whiskers.
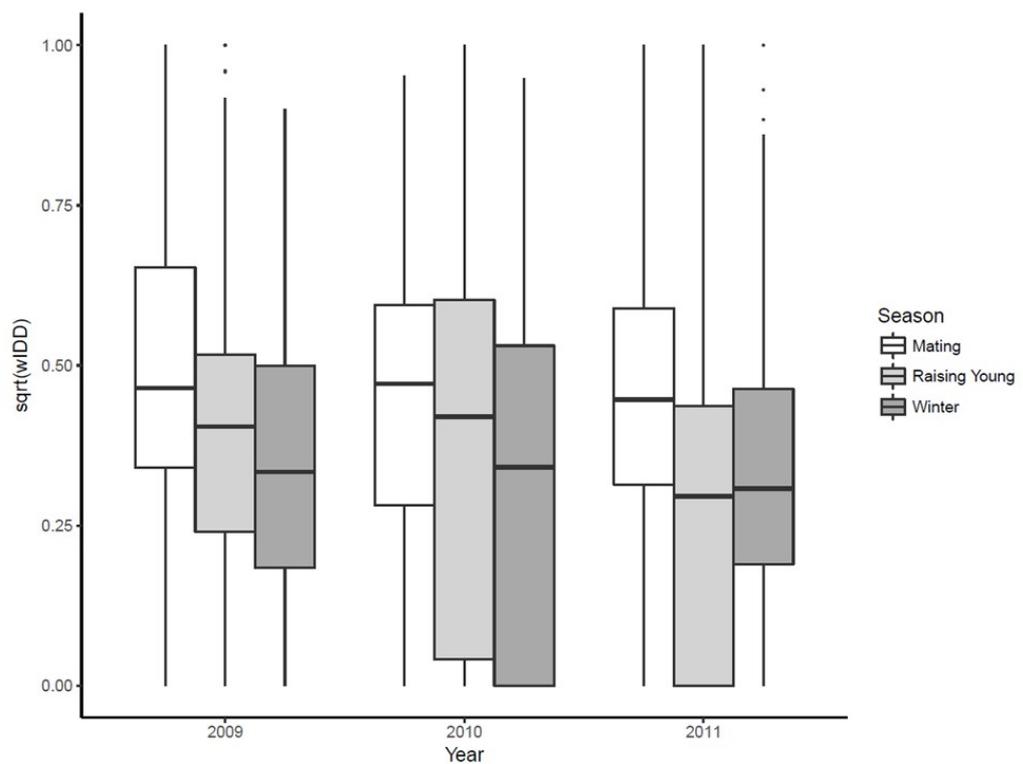
a.
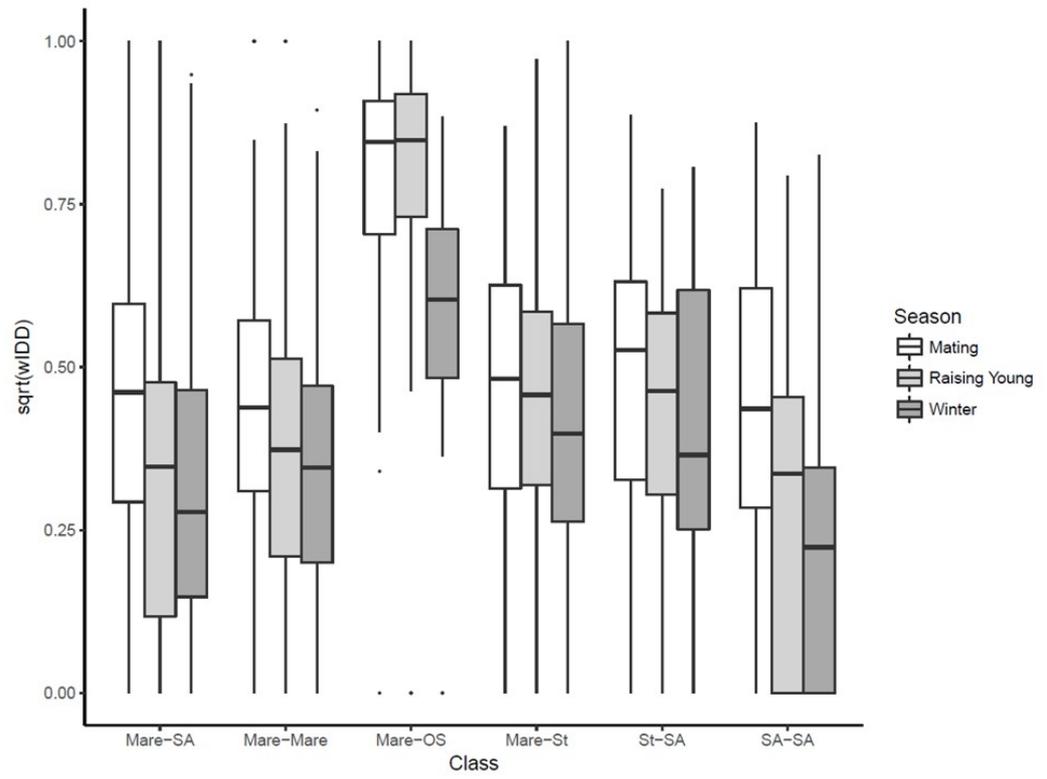
b.

Figure 2. Correlation coefficients between consecutive seasonal female pony proximity matrices. *X*-axis labels indicate pairs of seasons correlated (M = mating; RY = raising young; W = winter) and year (2009, 2010 or 2011). The grey shaded area is bound by the 95% confidence limits for these correlation coefficients.
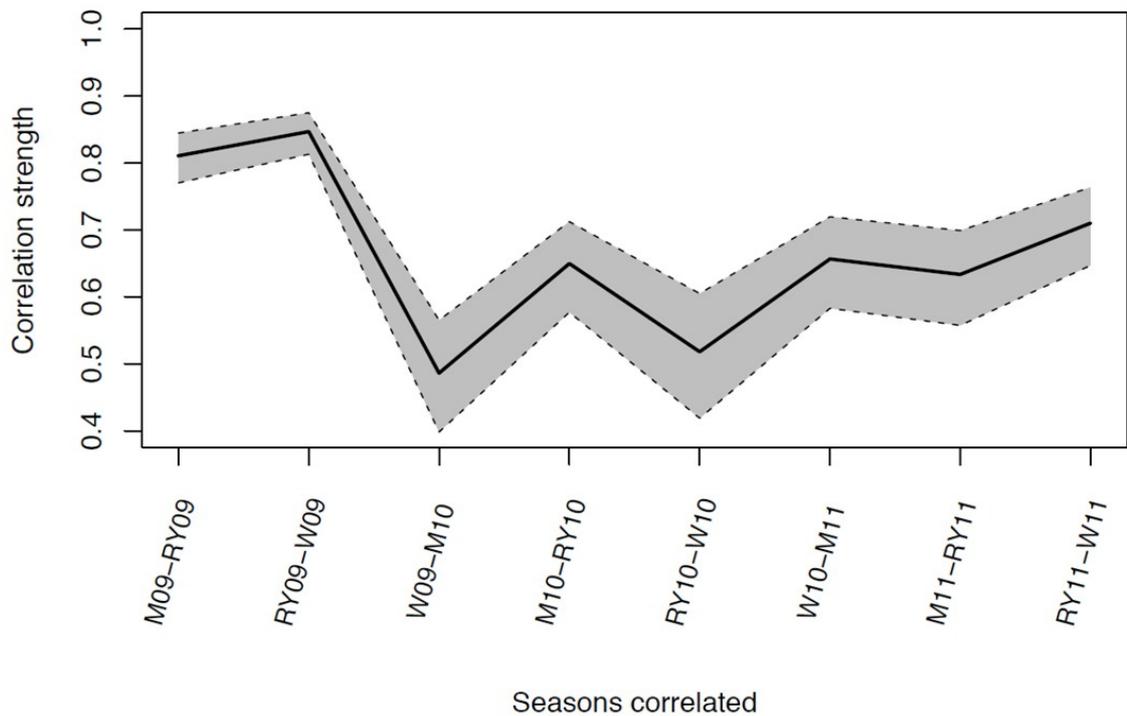
Figure 3. Seasonal effects on mean strength centrality in proximity networks for female ponies. Seasons: mating (April–June); raising young (July–September); winter (October–March). The boxes are bounded by the upper and lower quartiles and divided by the median. Maximum and minimum values within 1.5 box lengths of the quartiles are represented by the ends of whiskers.
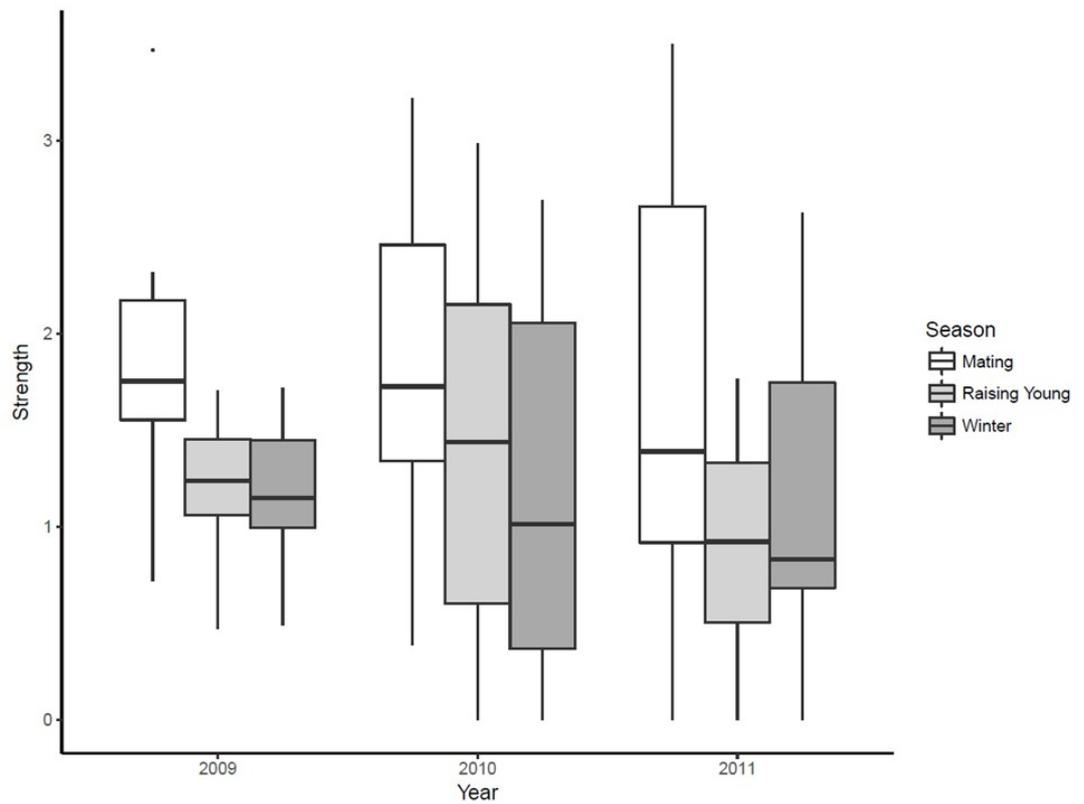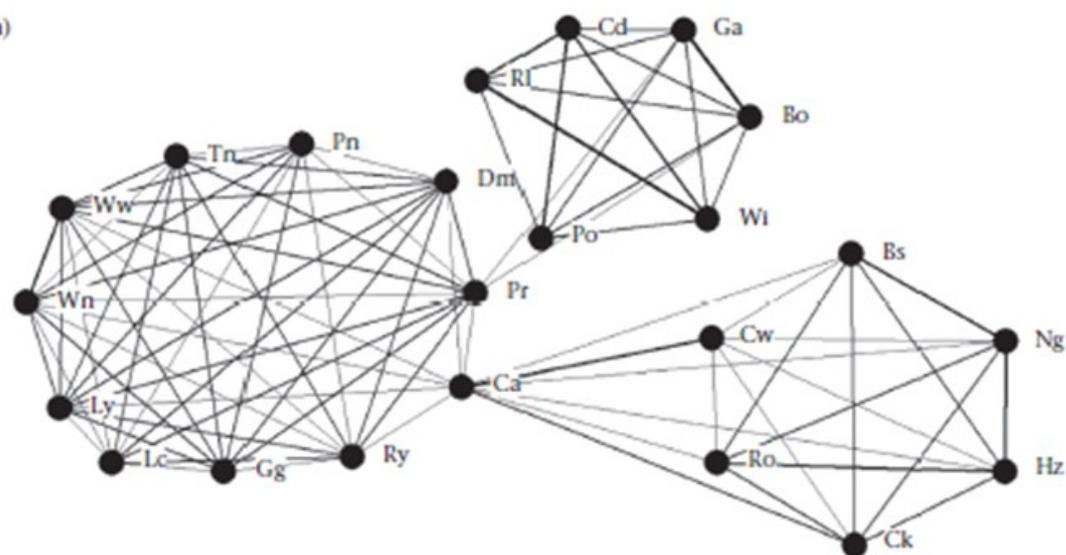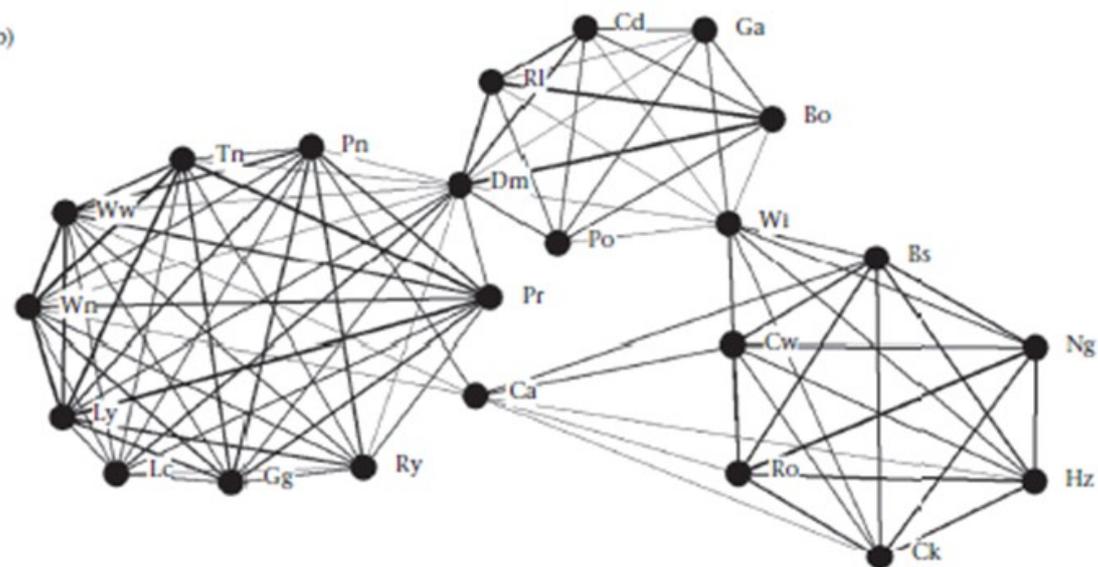
Figure 4. Annual female pony proximity networks built using weighted intradyadic distance (wIDD) as an association index for (a) 2009, (b) 2010 and (c) 2011. Labels represent individual IDs. Strength of line indicates bond strength, with thicker bonds indicating larger mean wIDD (i.e. closer mean proximity).

(a)

(b)

(c)