

Impact of group management and transfer on individual sociality in Highland cattle (*Bos ^taurus*)

Sebastian Sosa¹, Marie Pelé², Élise Debergue³, Cédric Kuntz³, Blandine Keller³, Florian Robic³, Flora Siegwalt-Baudin³, Camille Richer³, Peng Zhang¹, Amandine Ramos³, Cédric Sueur³

¹ Anthropology Department, Sun-Yat Sen University, Guangzhou, China

² Ethobiosciences, Research and Consultancy Agency in Animal Well-Being and Behaviour, Strasbourg, France

³ Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

Corresponding author: cedric.sueur@iphc.cnrs.fr, 0033(0)88107453, IPHC UMR 7178, 23 rue Becquerel F-67000 Strasbourg, France

Abstract: The sociality of cattle facilitates the maintenance of herd cohesion and synchronisation, making these species the ideal choice for domestication as livestock for humans. However, livestock populations are not self-regulated, and farmers transfer individuals across different groups throughout their lives for reasons such as genetic mixing, reproduction and pastureland management. Individuals consequently have to adapt to different group compositions during their lives, compared to their wild counterparts choosing their own herd mates. These changes may lead to social instability and stress, entailing potentially negative effects on animal welfare. In this study, we assess the how the transfers of Highland cattle (*Bos taurus*) impact individual and group social network measures. We studied four groups with nine different compositions and 18 individual transfers to study 1.) the effect of group composition on individual social centralities and 2.) the effect of group composition changes on these centralities. As shown in previous studies, dyadic associations are stronger between individuals with ~~identical~~ ^{similar} age and dominance rank. Our study showed that dyadic spatial relationships are stable relatively stable between changes in group composition or enclosure but this depends on ~~the~~ ^{the} identities more than the quantity of transferred individuals. Older cattle ~~have~~ ^{had} higher network centralities than other individuals. The centrality of individuals ~~is~~ ^{was} also affected by their sex and the number of familiar individuals in the group. When individuals are transferred to a group with few (one or two) or no familiar individuals, their social centralities are substantially impacted. This study reveals the necessity of understanding the social structure of a group to predict social instability through the transfer of individuals between groups.

The developing of guidelines for modifying group composition could improve livestock management and reduce stress for the animals concerned.

Keywords: livestock, social network, animal welfare, pastureland, farming, bovines

1. Introduction

Animal farming began in the Holocene (about 7500 years BC), when humans domesticated aurochs (*Bos primigenius*), the ancestor of *Bos taurus*. Humans mainly chose cattle because this species is social and this sociality facilitates the maintenance of herd cohesion and synchronisation, making it easier to locate the groups in pastureland and coordinate movements such as transhumance (Butt et al., 2009; Von Keyserlingk et al., 2008). In the wild, social groups are able to regulate their own composition: individuals migrate or groups split when competition for food becomes too high, for instance (Ruckstuhl and Neuhaus, 2000; Sueur et al., 2011b). This self-regulation is not possible in livestock. Farmers transfer individuals to different groups throughout their lives to facilitate genetic mixing and reproduction, or to manage pastureland activities (Bøe and Færevik, 2003; Gupta et al., 2008; Patison et al., 2010). Such changes may result in periods of social instability and stress (Estevez et al., 2007; Gutmann et al., 2015). These frequent changes in group composition modify the social organisation and stability of groups, with possible implications for animal welfare (Sueur and Pelé, 2015) and health (Costa et al., 2016).

Like their wild counterparts, domestic bovines show strong social behaviours with stable and long-term dyadic relationships, ^{when possible,} ~~meaning~~ ^{i.e.} when the group composition is also stable (Gutmann et al., 2015). Boyland et al. (2016) showed that cattle form strong relationships with specific partners. These preferential associations are dependent on different socio-demographic factors such as sex and age, as well as dominance, kinship or familiarity with other group members. Two individuals that are the same age or arrive in an enclosure at the same time will have a higher probability of developing a strong relationship than other individuals (Bouissou and Boissy, 2005; Bouissou et al., 2001). Many behavioural experiments have shown that cattle are able to discriminate between *familiar* and *unfamiliar individuals*, hereafter defined as individuals a bovine has spent time with, or unknown/new individuals, respectively (Hagen and Broom, 2003; Takeda et al., 2003). Adding new individuals to the group perturbs ^{this proximity} between familiars and aggressive ^{what does this refer to?} behaviour increases (Patison et al., 2010). This suggests that prioritising good and stable relationships in a group of animals enhances the wellbeing of ^{individuals} ~~animals~~ by decreasing their stress and stabilizing their social status indicated by dominance rank and social centrality. Farmers should consider using this principle in their livestock management (Bøe and Færevik, 2003; Boyland et al., 2016; Sueur and Pelé, 2015).

In physiological terms, this social stress may lead to decreased food ingestion, lower milk production and even ceased reproduction for cows (Bøe and Færevik, 2003), and can also have a strong impact on the behaviour, cognition and health of calves (Costa et al., 2016). This stress can be reduced by the presence of familiar individuals during transfer (Costa et al., 2015; Færevik et al., 2006). The impact of such transfers is also dependent on the sex of individuals: the removal of males

from an enclosure leads to stronger cohesion between females, whilst the removal of females does not influence associations between males, which remain basic due to the sexual segregation observed in cattle (Ruckstuhl and Neuhaus, 2000; Wilson et al., 2015). Females play the role of social cohesion in a group more than males, probably because they are the phylopatric sex, like in primates (Wrangham, 1980). Understanding the social structure of a group before transferring an animal appears necessary to predict any social instability caused by this change. Taking this factor into consideration would make livestock management more efficient and less stressful for animals (Bøe and Færevik, 2003). This study aims to assess how group composition affects social centralities of Highland cattle (*Bos Taurus*) and how the transfers of these individuals impact their social relationships using social network analysis to achieve this goal (Sueur et al., 2011a).

Highland cattle are originally from the Scottish Highlands in the United Kingdom. Like most domestic ungulates, this species is social with sexual segregation (Ruckstuhl and Neuhaus, 2000). This breed is particularly suitable for eco-pasturage due to its resistance to a large set of temperatures and its non-selective diet. Many French natural reserves and national parks have imported Highland cattle in order to maintain ecosystem biodiversity (Génot, 2000; Muller et al., 1998; Wintz and Fabien, 2012). The resulting number of Highland cattle populations with different group compositions facilitates a wide study permitting a more detailed understanding of how group compositions in terms of age ratio, sex ratio and group size affect the social centrality of cattle and how the transfer of individuals between groups impacts sociality and its dynamic in this species. We studied different compositions (nine in total) of four groups over a six-month period. We first assessed which sociodemographic factors (sex, age, dominance rank, and group size) influence the social centrality of Highland cattle, which was measured using eigenvector centrality (or popularity, i.e. how well an individual is connected to its neighbours, but also how ^{well} its neighbours are connected) and the strength of associations (or social activity, i.e. how often an individual is seen in the proximity of specific other group members) (Sueur et al., 2011a). In a second step, changes in group compositions in terms of group size, age or sex composition were examined to determine how they affected the associations of individuals and their social centrality. This enabled us to measure the changes in dyadic relationships and in individual centrality according to the changes in group composition.

Following the previous results on sociality in cattle (Hagen and Broom, 2003; Reinhardt and Reinhardt, 1981; Šárová et al., 2013), we expected social centrality to be influenced by the age, sex and dominance rank of group members and the number of familiars they have in the group. Older individuals were expected to have a higher dominance rank and a higher social centrality. Familiar individuals or those of the same sex and age should also show stronger dyadic associations. After a transfer, fewer changes in eigenvector centrality and strength of associations were expected in older,

dominant individuals, whilst the opposite was expected in younger, subordinate individuals in the new group composition. Concerning ~~the~~ familiarity, we expected that individuals ^{comparatively} having a ^{higher} number of familiar individuals ~~comparatively~~ (for instance three or four) ^{would} see their social centrality less impacted than those that had no or fewer familiars (for instance one or two). ^{We further predicted that} Resident individuals, i.e. those who experienced the arrival of a newly transferred individual in their group, ^{would} ~~should~~ be less impacted than those being transferred (Patison et al., 2010). We suggested that the number of transferred individuals is not the only one to have an impact on the social relationships but the social role of removed or newly added individuals can have strong consequences on the social structure. We expected that the removal or addition of specific individuals such as a bull or an older individual, specifically an older female, may strongly impact the social relationships of all other individuals because of its specific social role inside the group.

2. Material & Methods

a. Ethical Note

This study was based on the observation of animals, and no handling or invasive experiments were involved. Our study was approved by our research institution (Institut Pluridisciplinaire Hubert Curien). It was carried out in full accordance with IPHC ethical guidelines and complied with European animal welfare legislation. Every effort was made to ensure the welfare of the animals and minimize disturbance by researchers present in the field.

b. Observation sites and study subjects

this does not make sense as written: one should add what it would have an effect on

We studied the **effect of group composition and of group composition changes** in four groups of Highland cattle (Table 1). We mean by group composition change that a minority of the individuals changed at the study location (Robertsau, Niedersteinbach, and Sturzelbronn), either by adding some new individuals, ^{or} ~~either~~ by removing some individuals from the group. The four groups were located in the Grand Est region of France (see the supplementary information file for a map of the different locations). Group composition changes were made by the farmer, either for the needs of farmland management or for breeding reasons. ^{In particular} ~~Particularly~~, the non-castrated bull was transferred between the groups in order to copulate with females. The castrated bulls ~~in another way~~ ^{also} were introduced with juveniles in order to decrease the stress of the latter and because bullocks are known to be less aggressive than bulls (Bouissou, 1983; Delville et al., 1996). Juveniles were transferred to make their ^{reproductive?} ~~reproducible~~ mother ~~reproducible~~ again. When females were transferred, the reason was more for pastureland management (Génot, 2000; Muller et al., 1998; Wintz and Fabien, 2012). The authors did not have ^{input} ~~weight~~ in the management decision, either for the time of transfer or for the individuals to

transfer. However, among 25 groups of Highland cattle available in the Vosges (France), from three to about 20 members, we choose to study specifically these four groups for their group size and their different group composition (only females with juveniles, females with a bull, juveniles and bullocks; females with different versus similar ages). Group size was chosen to be high enough to perform social network analyses (in the other way, differences of centrality are not strong enough to highlight which individual factor affects social relationships). Group compositions were chosen in order to study first the impact of group composition on individual social centrality and second to study how the changes of group composition affect these centralities.

Water was supplied via a water pump for the Robertsau group, whilst the three other groups had access to a river. Enclosures were all composed of similar vegetation: mainly grass (more than 90% of groundcover), wetland, some bushes and some small areas of forest, as indicated in the figures of the supplementary information file. Animals were supplied with hay during winter. Hay was dispersed twice a week on a surface area of about seven acres to avoid resource competition. Observations were carried out over two periods: one in 2015, from April 14th to August 28th, and the second in 2016, from January 22nd to April 29th. During the two periods, the composition was changed in all groups except the Rolbing group (Table 1). Each group member was identified according to physical traits such as coat colour and horn shape. These physical traits had been clearly identified for each individual prior to the study.

c. Changes in group composition

Group composition changes are summarised in Figure 1. A total of nine group compositions were observed for these four groups (Table 2) involving 18 individual transfers:

- Robertsau (Rob) group (3 group compositions): The group was initially composed of 14 female individuals (nine 3yo (year old) individuals and five 2yo individuals). On the 21st March 2015, seven females (two 2yo individuals and five 1yo individuals) were added to this initial group. During the second observation period, 13 individuals were removed from the group (eight 3yo individuals, four 2yo individuals and one 1yo individual) and three 2yo females were added (originating from groups other than those studied here), forming a group of 12 females (one 4yo individual, three 3yo individuals and eight 2yo individuals). We also observed four enclosure switches (change of enclosure and change of enclosure size, decided by the farmer), which had no connection with changes in group composition and were made for feeding and farmland reasons. These enclosure switches were observed on 30/06/15, 21/07/15, 17/02/16 and 08/04/16 and were taken into account in the statistical analyses.

- Niedersteinbach (Nie) group (two group compositions): The group was initially composed of ten individuals (one 7yo male, eight 5yo females and one juvenile female). The male was removed from the group on the 2nd June 2015 and was added to the Stu group.
- Sturzelbronn (Stu) group (three group compositions): The group was initially composed of 18 individuals, namely 15 females (one 13yo, two 8yo, three 7yo, two 6yo, four 2yo and three 1yo individuals) and three 1yo males. Ten individuals were removed on the 25th May 2015, namely the three 1yo males, four 2yo females and three 1yo females. An adult male (7yo) was added to the group on the 2nd June 2016.
- Rolbing (Rol) group (one group composition): the group ^{was} ~~is~~ composed of 11 individuals, namely two castrated males (2yo), two young females (1yo) and seven young males (1yo). Its composition did not change during the study.

d. Data scoring

Data were scored by two observers located two to ten meters from the animals. The two observers were always ^{within} ~~at~~ ^{of} ~~one-meter~~ each other, one observing and indicating the behaviours to the second observer writing or implementing them. This ~~also allowed to double-check behaviours~~ ^{to be confirmed by two observers}. Cattle were already habituated to human presence and were not disturbed by the observations, which were made once a week over a six-hour period between 9am and 5pm. The groups were not observed during rainy or snowy days and not during the week-ends. Sampling frequency for each group composition is given in table 2.

The group social network was defined and scored using dyadic spatial associations (Boylard et al., 2016; Sueur and Pelé, 2015). Spatial associations were defined according to the nearest neighbour (closest individual whatever the distance) and were scored every five minutes with the instantaneous sampling method (Altmann, 1974). This means that every five minutes (one scan), we recorded as “1” in a matrix if individual A was the nearest neighbour of individual B and “0” if it was not. We summed all scans in one matrix for each group composition giving us absolute frequencies of nearest neighbours. We called dyadic spatial association the absolute frequency of nearest neighbour between each dyad of group members. The total number of scans is indicated in Table 2. When evaluating social group network, it is better to use the “nearest neighbour” approach than the “five-meter proximity” concept, as the latter is complicated by a “gambit of the group” issue, meaning that the individual C is maybe at less than five meters from the individual A, not because C is associated to A but because C and A are both associated to another individual B (Farine and Whitehead, 2015; Franks et al., 2010). In this way, the nearest neighbour approach implies less “noise” than the five-meter proximity one. Spatial proximity matrices and nearest neighbour

matrices are highly correlated (Mantel test with 1 000 permutations: $r \geq 0.78$, $p \leq 0.0001$). Given these two points, we chose the “nearest neighbour” approach to measure associations.

Observers also scored spontaneous agonistic interactions using the behavioural sampling method (Altmann, 1974) in order to assess the dominance hierarchy of each group composition. We scored supplant, avoidance and aggression as agonistic interactions. We measured each agonistic interaction as an event whatever the time of the interaction. We scored as 1 this interaction between individual A and individual B in a matrix of agonistic interactions. We then summed all dyadic agonistic interactions for each group composition period. Agonistic interactions, considered to be the best choice of dominance index (de Vries et al., 2006; Gammell et al., 2003), were used to calculate the Modified David Score. David’s score is based on an unweighted and a weighted sum of the individual’s dyadic proportions of wins combined with an unweighted and a weighted sum of its dyadic proportions of losses (de Vries et al., 2006). Animals that usually dominate have high positive scores, and those that are usually dominated have largely negative scores. Individuals were ranked from the highest MDS to the lowest one: the individual with the highest value were ranked first whilst the individual with the lowest value was ranked last in the dominance hierarchy. SocProg 2.6 (Whitehead, 2009) was used to calculate the Modified David Score for each group composition, and scoring began on the eighth day following transfer. We did not take into account the first days of observations in our calculation because of the instability of social and hierarchical relationships. Whilst the number of aggressions were higher during these first days compared to stable periods, many agonistic behaviours were bidirectional, meaning that the hierarchy was still not established. These agonistic behaviour did not fit with the dominance ranking we observed in the stable periods.

Basing our analysis on the time intervals between group composition changes during our observation periods, we defined familiarity as the number of familiar individuals in the group, meaning the number of individuals a group member is with / has been with for more than three months (Sueur et al., 2017). The examination of the pedigree for each individual revealed that kinship association matrices would be difficult to obtain for each group composition due to missing data or very close genetic proximity between familiar individuals. We therefore preferred to analyse familiarity and did not assess the effect of kinship. Moreover, group composition change is the reason why familiarity is studied more frequently than kinship in applied studies in ungulates (Færevik et al., 2006; Gutmann et al., 2015; Hagen and Broom, 2003; Patison et al., 2010; Takeda et al., 2003).

e. Social network analysis

Social network analysis (SNA) is an increasingly widespread tool for the study of sociality and its dynamic (Croft et al., 2008; Farine and Whitehead, 2015; Pinter-Wollman et al., 2013; Sueur et al.,

2011a). Indeed, social relationships can change with time because of changes in social strategies of group members, arrivals or departures of individuals (births, deaths, migrations or transfers). Specific tools were developed in SNA to analyse these changes and their causes (Borgeaud et al., 2017, 2016; Boucherie et al., 2017; Pasquaretta et al., 2016). However, SNA is also recognised now as a tool for animal welfare and conservation (Koene and Ipema, 2014; Snijders et al., 2017; Sueur and Pelé, 2015). We added together the matrices of spatial associations obtained per observation day for each group composition. In this way, each dyad of individuals obtains a spatial association weight indicating whether or not these two individuals were frequently observed together. The spatial associations for each group composition were used to calculate the eigenvector centrality coefficient and the strength of associations of each individual (Sueur et al., 2011a). These measures were calculated using SocProg 2.6 (Whitehead, 2009).

Eigenvector centrality is a commonly used measure of individual centrality, indicating popularity (Kasper and Voelkl, 2009). This coefficient is defined as a measure of how well an individual is connected to its conspecifics, and also reveals the connections of the group members to which it is connected (Bonacich, 2007).

The strength of associations is the sum of each node's edge values and indicates social activity (Kasper and Voelkl, 2009). The individual with the strongest and most numerous associations has the highest strength value (Sueur et al., 2011a). In our study, strength indicates the number of times an individual was observed as the nearest neighbour of another individual. Indeed, in a given scan sampling, one individual might be observed several times as the nearest neighbour of its group members (maximum = $N - 1$, where N is the group size).

These two variables are correlated but are far from collinear (Pearson correlation test, $r=0.16$, $p=0.03$).

f. Statistical analyses

1. Effect of socio-demographic factors on dyadic spatial associations: We first assessed how the weight of dyadic spatial associations was influenced by socio-demographic factors such as sex, age and dominance. A Mantel test with 1 000 permutations was used to make matrix correlations to check whether individuals sharing similar characteristics (similar age, dominance rank or sex) have stronger dyadic associations than individuals that do not share similar characteristics. This is called homophily, i.e. the tendency of individuals to associate and bond with similar congeners (Massen and Koski, 2014; McPherson et al., 2001). Using Socprog 2.6, we then created matrices for age differences (0 means that dyad's individuals have the same age, 1 means that they have a difference of one year about their age, and so on), dominance rank differences (0 means that dyad's individuals have the same rank, 1 means that they have a difference of one dominance rank, and so on) and sex

difference (0: same sex, 1: different sex). These three matrices were calculated for each group composition and correlated to the dyadic spatial associations' matrices for each group composition.

For each socio-demographic factor, we combined the p-value of all group compositions to obtain global statistics using the 'CombinePValue' package in R.

I am not sure what the authors have done here—I am not familiar with this approach. Could the authors elaborate in one or two sentences? ~~Could the authors elaborate here on how they combined the p-values?~~

2. Effect of changes (group composition or enclosures) on dyadic spatial associations: We also correlated the dyadic associations' matrices after a change (transfers or enclosure change) keeping only for each matrix individuals present into the two adjacent matrices (ex: Rob1-Rob2, Rob2-Rob3, Stu1-Stu2, etc.). We used a Mantel test with 1 000 permutations in SocProg 2.6. We then correlated the correlation coefficient with the number of individuals transferred between two group changes using a Spearman correlation test with permutations (library R "Coin").

Generalized Linear Mixed Effect Models (GLMMs):

1. Effect of group composition on individual social centralities: GLMMs (R package 'lme4'; Bates et al., 2014) were used to test whether the eigenvector centrality and the strength of associations were affected by the following independent sociodemographic variables: the age of individuals, their sex, their dominance rank and the number of familiar individuals they were associated ~~to~~ ^{with} in the group. The experimental units we used were the eigenvector centrality for a first GLMM and the strength of associations for a second GLMM, per individual and per group composition. Prior to GLMMs, the eigenvector centrality and the strength of associations were corrected using the group size for each composition in order to control for the mathematical effect of the number of nodes on network metrics. For the regression $y=ax+b$, we multiplied y (the eigenvector centrality or the strength of associations) by b . The identity of individuals was included as a random factor.

2. Effect of group composition change on individual social centralities: We also carried out two GLMMs using the differences in eigenvector centrality and in the strength of associations between two compositions, as positive or negative values. The experimental units we used were the eigenvector centrality difference for a first GLMM and the association strength difference for a second GLMM, per individual and between two group compositions. Effect variables were the age of individuals, the number of familiar individuals in the new group, the difference in dominance rank between the two compositions (negative or positive values) and the total number of added or removed individuals. The identity of individuals was included as a random factor. We did not include the sex variable in this last model testing the differences between two group compositions as only four males (one adult and three juveniles) were transferred to another group, meaning that the sample size was too low ~~to have an effect~~, and this variable was correlated with the age of individuals

in the model (the male was the only adult during the transfer, same for the juveniles for another transfer).

We did not include the period as random factor in our GLMMs because the variation of temperatures between the two periods (period 1 and period 2) was inferior to the difference of temperatures during a day (Independent sample test with permutations: $z=4.76$, $p<0.0001$) and because the social behaviour of cattle did not change during the daytime (The changes in dyadic associations between period1 and period 2 is not higher than the changes inside each period: $r=0.6$ versus $r=0.58$). Even if the activity changes with the temperature, the social behaviour does not (Sueur et al., 2017). In addition, the period is confounded with the group composition and we already took into account the group composition in our model. Taking both factors into account could lead to false interactions influencing the statistical significance of our results (false positive or false negative, Pourhoseingholi et al., 2012).

For each GLMM, multi-model inferences were run to compare and rank candidate models according to (i) their respective Akaike Information Criterion (AIC) after correction for small sample sizes (AICc) and (ii) normalized Akaike weights (AICw) (Burnham and Anderson, 2004). This means that for each combination of factors, all models were tested and ranked according to the best AIC. $\Delta AICc$ is the difference in AICc between a given model and the model with the lowest AIC. The AIC weight indicates the probability that a given model will be the best among candidate models. Models with a $\Delta AICc < 10$ were considered equally possible candidates, and their statistics were averaged. The null model (random effect: identity of individuals) was included as a possible candidate but was never among the models with lowest AICc. We also indicated in the results the relative variable importance (RVI), which is the number of times a variable is present in the best models. Model inference and averaging were carried out with the R package 'MuMIn' (Bartoń, 2013). Node label permutations were also performed (Croft et al., 2011; Farine, 2017). Permutations are a robust and modern standard way to do that is to compare statistical models based on the original observed data to a distribution of null models based on randomised data (Farine, 2013; Farine and Whitehead, 2015). After 1000 randomisations, the statistical parameters of interest (e.g. model estimates) of the models based on observed data were compared with "null" models based on randomised data. If a substantial proportion (95%) of the statistical parameters derived from models based on observed data were lower/higher than parameters derived from models based on randomised data, then we could conclude that the observed effects^{on? of?} sociality were different from those expected to arise by chance. The randomisation procedure is exactly the same for all analyses. The P-values indicated in the tables were based on these permutation procedures. GLMM diagnostics (i.e. residual normality distribution plot and multicollinearity between dependent factors) were carried out to evaluate the

validity of the final models. We checked for multicollinearity of the predictor variables by calculating the variance inflation factor (VIF, R package 'car', Fox et al., 2007). In all cases, the predictor variables had a VIF value ranging from 1.02 to 1.9, indicating that the predictor variables were not correlated. The significance level was set at 0.05. Statistical analyses were performed in R 3.24 (R Development Core Team, 2009). Plots of residual normality distribution can be found in the annexes (Table S1).

3. Results

We ~~have to~~ note that in his way to manage the group, the farmer usually transferred young individuals. Young individuals are usually dominated by older ones in cattle (Pearson correlation test for our data: $df = 176$, $r = -0.37$, $p < 0.0001$). Moreover, individuals arriving in a new group have ~~less~~ ^{fewer} familiar individuals and get a dominance rank lower than resident ones (Pearson correlation test for our data: $df = 111$, $r = 0.41$, $p < 0.0001$), not because of their low number of familiars but because resident individuals are usually dominant on newly transferred ones. We discussed ~~ed~~ this in the discussion ~~part~~.

a. Do dyadic spatial associations depend on shared characteristics among dyads?

Table 3 indicates the results of correlations ~~s~~ tests between the dyadic association matrices and those of characteristics differences. Fig. 2 shows four instances of Highland cattle social networks. A relatively high variability is observed according to group composition. There is a significant correlation between matrices of dyadic associations and of dominance rank differences. Most correlations are negative, indicating that close-ranking individuals have stronger associations than individuals with distant ranks. This is illustrated by the social networks in Fig. 2a and Fig 2b. Dyadic associations ~~are~~ ^{were} only dependent on the sex of individuals in the Rolbing group, where individuals of the same sex ~~have~~ ^{had} stronger associations (Fig. 2b). However, dyadic associations are mostly negatively correlated with age difference, ^S_A indicating that individuals of the same age have stronger associations than cattle with greater age differences (greatest difference represented in Fig. 2c). The results for age and dominance led us to make correlations between matrices of dominance and age difference. Results show that individuals of a similar age also share similar ranks; VIF analyses based at the individual level do however show that these two factors are not collinear (see Statistical analyses in the Methods section).

b. How does a change of group composition or of enclosure affect dyadic spatial associations?

The correlation coefficients concerning periods before and after a change ranged from -0.03 to 0.69 with an average of 0.47. This average is lower than we expected and means that 47% of relationships are stable after a change whilst 53% change significantly. This correlation coefficient is not significantly affected by the number of transferred individuals ($r=-0.49$, $z=-1.4$, $p=0.169$). Hereafter we detailed this result for each group. After the removal of the male, the dyadic spatial associations of the Niedersteinbach group did not change significantly ($r=0.52$, $p=0.0002$). Dyadic spatial relationships in the Robertsau group seemed to stay stable after a change, ~~whatever if~~ **regardless of whether** it is a change of enclosure or of group composition ($0.69 > r > 0.52$; $p < 0.0001$). Finally in Sturzelbronn, results are quite different from the two previous groups with no significant stability of dyadic spatial relationships. The correlation coefficient after the removal of juveniles is -0.03 ($p=0.812$) showing a strong instability of mothers' relationships after the removal of their offspring. Similarly, the dyadic spatial relationships after the addition of the bull into the group are not correlated significantly to the ones before this addition ($r=0.14$, $p=0.426$) meaning that the male might have ^astrong impact on females' relationships.

c. How do sociodemographic factors influence individual centralities?

The model selection for eigenvector centrality is indicated in Table S2. The three variables retained in the best models are dominance, familiarity and age. However, the relative ~~variable~~ importance of these variables is low ($RVI(\text{dom})=0.23$; $RVI(\text{famil})=0.04$; $RVI(\text{age})=0.01$) and after permutations, none of these variables have a significant influence that could explain the variance of the eigenvector centrality (Table 4).

The model selection for the strength of associations is indicated in Table S3. The variables retained in the best models are dominance, familiarity, sex and age. Familiarity (i.e. the number of familiar individuals in the group) has a strong and significant influence on the strength of associations ($RVI=0.99$, Table 5, Fig. 3), i.e. the more familiar cattle an individual has, the stronger its strength of association will be. Females also have significantly lower strengths of association than castrated males ($RVI=0.89$, Table 5, Fig. 4). Finally, age has a significant influence on the strength of associations ($RVI=0.12$, Table 5), with higher strength values in older individuals than for younger ones.

d. How do changes in group composition affect individual centralities?

The model selection for the difference of eigenvector centrality after a transfer is indicated in Table S4. The three variables retained in the best models are dominance, familiarity and age. However,

only age has a significant influence ($r_{vi}=0.05$, Table 6), with the eigenvector centrality of older individuals increasing whilst that of younger individuals decreases (Fig. 5).

The model selection for the difference of strength of associations after a transfer is indicated in Table S5. The variables retained in the best models are dominance, familiarity in the new group, age, and the number of transferred individuals. However, only the number of familiar individuals in the new group had a significant influence on the difference of strength of associations ($RVI=1$, Table 7), with individuals that had greater numbers of familiar individuals showing stronger strengths of associations (Fig. 6).

4. Discussion

This study shows how individual and dyadic social network metrics are shaped by sociodemographic factors and composition changes in several groups of Highland cattle. Analyses of dyadic associations and individual centralities highlighted correlations between ~~the triad proximities~~^{spatial} and age, dominance, an influence of familiarity, age and sex on individual centralities, and finally an impact of transfers which mainly varied according to the number of individuals with which the transferred animal was already familiar.

a. How do sociodemographic factors and group composition influence dyadic associations and individual centrality?

Matrix correlation tests revealed that individuals of similar age and dominance rank develop stronger associations and are found closer to each other than individuals of different age and sex. However, the tests also showed a correlation between age and dominance rank similarities. For instance, individuals 951, 949 and 947 in the Robertsau 6 group composition (Fig 2a) are approximately the same age, are the top-ranking individuals and form a triad with strong associations. This configuration has also been reported in female mouflons (*Ovis gmelini*) where the most dominant females form triadic relationships (Guilhem et al., 2002; Le Pendu et al., 2000). This brings “triadic closure” to mind, a mechanism that may facilitate the development of cooperation for social alliances or access to food. However, it is not clear whether triadic closure is a by-product of socio-demographic characteristics (i.e. individuals that share the same characteristics also share the same needs), or if it is a social strategy leading to better cooperation between multiple partners (Banks and Carley, 1996; Righi and Takacs, 2014). Other instances in Figure 2 also show this homophily according to age and dominance (Lusseau and Newman, 2004; Massen and Koski, 2014). Many authors have confirmed homophily (tendency of individuals to associate and bond with similar

others) in ungulate species (Gerard and Richard-Hansen, 1992; Guilhem et al., 2000; Kimura, 1998; Roberts and Browning, 1998; Winfield et al., 1981), and underline ~~the fact~~ that animals with the same socio-demographic characteristics ^{may} also share the same social or physiological/nutritional needs. Indeed, younger individuals show strong associations, as observed in the Rolbing (and Sturzelbronn 1) group compositions (Fig. 2b and Fig. 2c, respectively). This homophily in young individuals seems to be important for them to learn how to live in groups and acquire sociality without risk of injury particularly when in contact with adults (Shimada and Sueur, 2014). The same reasoning about reducing risk of injury could be applied for homophily between individuals that have the same dominance rank. Risk of injury prevents subordinate individuals from having strong associations with dominant individuals (for examples, see Syme et al. 1975 for an example in ungulates and Balasubramaniam et al., 2012; Borgeaud et al., 2016; Sosa, 2016 for primates). This dominance-related homophily may also result from competition between individuals to associate with top-ranking individuals to obtain tolerance or access to resources. However, as high-ranking individuals are already associated among themselves, low-ranking individuals might not gain access to them (Borgeaud et al., 2016). The results we obtained were not observed in all group compositions, and ^{could be} this ~~is~~ explained by intra-group age variance. The difference in dominance and the strength of homophily increase with ^{differences in age} ~~age difference~~. This was seen in the Niedersteinbach group, where the maximum age difference between individuals was two years (individuals aged 7yo and 5yo, with the exception of one juvenile). Unlike the other compositions, no age-related homophily was observed in this group.

Individuals of the same age also have more similar dominance ranks than individuals of different ages. Age affects dominance through the association of individuals, meaning that individuals of the same age are also likely to develop the same dominance rank because of their strong and close associations. Social status such as dominance increases with age through ^{different} ~~difference~~ processes such as increases in body weight, experience and knowledge or social power (Crockford, 2016; McComb et al., 2011; Šárová et al., 2013; Sosa, 2016; Tokuyama and Furuichi, 2017). In the Niedersteinbach 1 group composition, the male, which ^{was} ~~is~~ also the oldest and highest-ranking individual, ^{played} ~~plays~~ an important role in the correlation with dyadic associations. The correlation ^{was} ~~is~~ no longer significant when this individual ^{left} ~~leaves~~ the group (Niedersteinbach 2). This is either simply because it has been removed from the statistics, or because the group's social structure has been perturbed. When this male arrived in the Sturzelbronn 3 group composition, it was no longer the oldest in the group but it became the highest ranking individual, making the correlation with dominance and associations significant.

Whilst age and dominance have a strong impact on dyadic relationships, we found that age was the only variable affecting strength of associations. Older individuals obtain stronger strengths of associations, but dominant individuals do not. There does not appear to be any competition for the central positions in the groups we studied. Dominant individuals are usually expected to develop strong associations because they occupy central positions in the group for better protection against predators or increased access to other resources. This affords higher centrality to these dominant individuals than to others. ~~The term 'other resources' refers to~~ ^{in this system were} small clumps of trees that protect from the sun and high temperatures, ~~as we observed in Highland cattle.~~ ^{we observed that} These spots are appreciated by animals for thermoregulation, and dominant individuals particularly defend them from the presence of others: (Laforge et al., 2016; Lopes et al., 2016; McCann et al., 2016). Whilst some such areas were present in our study groups, we did not observe any related socio-spatial correlation. This was probably due to an absence of competition between group members.

Centrality is also linked to age, with the oldest individuals having the highest strength of associations. With age, individuals become more and more selective (Almeling et al., 2016) in their social relationships. Young individuals interact unselectively with many partners in order to learn social rules (Shimada and Sueur, 2014). With time, they develop more stable relationships and become more and more central (Sosa, 2016). In our study, this effect was amplified because young individuals, juveniles or young adults were also those the farmers chose to transfer. They therefore had to develop new relationships each time they were transferred, accentuating the link between age and centrality. Juveniles usually have strong relationships with their mothers, yet few juveniles were still in the presence of their mother in our study. They were not easily accepted on their transfer and remained on the periphery of the new group, forming strong dyadic associations among themselves as already shown in previous studies (Bøe and Færevik, 2003; Raussi et al., 2010). This result for age is emphasised by that obtained for familiarity. Indeed, in our study, familiarity was ~~quite~~ ^{stayed} linked to age as older individuals ~~staid~~ ^{stayed} in their enclosure whilst younger ones were transferred. Individuals with a greater number of familiar individuals in the group showed higher centralities. In bovines, group members form subsets of familiar individuals, accentuating dyadic relationships and increasing centralities (Gutmann et al., 2015; Sato et al., 1993). In sheep (*Ovis aries*), familiar individuals are attracted to each other, whilst non-familiar individuals are not (Winfield et al., 1981). In our study, resident cattle rebuffed new individuals and were more aggressive to them around ^{(personal observations)?} coveted spots. The same result has been found in barnacle geese (*Branta leucopsis*) (Kurvers et al., 2013) and in mallards (*Anas platyrhynchos*) (Bousquet et al., 2017).

Sex also affected the strength of associations in our study, with castrated males showing stronger strengths of association than females. We did not observe any difference between males and

females, and this is mainly due to the social organisation of bovines. Bovines show sexual segregation, and females usually develop stronger and more stable dyadic associations than males, resulting in a higher centrality for females (Bouissou et al., 2001; Reinhardt and Reinhardt, 1981; Villaret and Bon, 1998). However, the fact that male juveniles remain closer to their mother and other young individuals affects this sex-centrality link in our study. The stronger centralities of the two castrated males in our study are mainly explained by the group composition. These two individuals were the two only adults in a group of juveniles, which seek for higher group cohesion than adults. The sex variable was thus confounded with age in the Rolbing group, and this probably explains why we obtained this result in our study.

Eigenvector centrality was not affected by any of the factors we studied. This is probably because eigenvector centrality takes not only direct connections (i.e. how an individual is connected) into account, but also indirect connections, i.e. how its neighbours are connected to other individuals (Bonacich, 2007). Our studied groups were quite cohesive with a low sample size, which may have led to a low variance of eigenvector centralities between group members and an absence of correlations with socio-demographic factors.

Together, these results allow us to identify which factors affect the social relationships and thus the centralities of group members; combining these factors might be used as a tool to reinforce group cohesion, by giving a key sociality role to one specific group member or decreasing aggressiveness during group transfers.

b. How do transfers influence dyad associations and individual centralities?

Our results showed that the identities of transferred individuals more than the quantity seem to affect social relationships. Indeed, the addition ^{or} ~~of~~ the removal of young or adult individuals not related to other group members do not seem to significantly affect the social relationships of resident individuals, except with the addition of the male in Sturzelbronn. However, the removal of the offspring seems to destabilize strongly the relationships of the mothers.

The difference in the eigenvector centralities between two transfers is explained by age alone. Results show that the centrality of young individuals tends to decrease during transfer, whilst older individuals obtain higher centrality. During transfer, most young individuals leave their original group for a new group where their mother is absent. These individuals are then isolated and placed at the periphery of the group until they form new and stable relationships (Færevik et al., 2006). Inversely, adults benefit from the transfer of young individuals as they are residents, and newly transferred individuals are seeking cohesion to alleviate their stress. Indeed, stress increases social cohesion and proximity with partners (Dufour et al., 2011; Hansen et al., 2009; Heathcote et al., 2017). Moreover,

the eigenvector centrality coefficient takes into account not only the connections of a group member, but also how these connections are connected to other individuals in the group (Bonacich, 2007). Indeed, if the relationships of an individual change but those of its connected individuals do not, then little change will be seen in eigenvector centrality, whilst strength of association will increase/decrease. In this respect, the eigenvector centrality coefficient is more stable than coefficients that are solely focused on the individual, such as strength of associations or degree (Levé et al., 2016).

Strength of associations was only affected by the number of familiar individuals in the new group. Individuals with a stable number of familiar individuals in the new group composition showed frequent interaction with them, whilst the individuals that had been separated from familiar individuals interact less with other group members and ~~need~~^{needed} time to develop strong and stable associations. Færevik et al. (2006) showed that the presence of familiar individuals during transfer is indeed less stressful. Familiar individuals have a stronger strength of associations due to increased group cohesion (Dufour et al., 2011; Hansen et al., 2009). Finally, and surprisingly, the number of transferred individuals did not lead to a change in strength of associations. Mathematically, as there are more partners to associate with when the number of individuals increases in a group, there is less possibility to associate per partner. We should therefore observe a global decrease in the strength of associations per individual. Kondo et al. (1989) showed that an increase in group size may lead to decreased space availability and therefore result in a higher occurrence of agonistic behaviours. The fact that we did not observe such an effect in our study, at least after removing the first eight days after a transfer, could be explained by the large size of the enclosures. Indeed, aggressive interactions are at their highest when the groups are first mixed. In most cattle groups, once the dominance rank is established aggression is rarely seen as groups operate more on affiliative than agonistic behaviours (Schein and Fohrman, 1955). Newly transferred individuals in this study have usually all been removed from the same group, and this may lead these individuals to stay together (resident vs. transferred), meaning that there is no change in their relationships. However, this hypothesis remains to be tested as even if they stay amongst themselves, the stress entailed by the change should lead to a greater cohesion of individuals, and this was not observed in our study.

c. Implication for animal welfare

Our results show that a group is structured according to age, dominance and familiarity. Favouring specific difference of age between individuals and subsets of familiars may be a tool to control cohesion and stability and decrease aggression in a group. The individual centralities of cattle decrease during transfers and changes in group composition. This occurs mainly in young individuals and is due to the loss of familiar individuals. During stressful events, animals seem to prefer to

interact with familiar individuals and avoid interacting with unfamiliar group members (Winfield et al., 1981). When transferring individuals, it is therefore preferable to select a certain number of familiar individuals to transfer as a group in order to decrease stress. Although it is true that animals should adapt to their new environment after a certain time (Estevez et al., 2007) an optimal group composition will permit ~~the faster the adaptation~~ ^a ~~the~~ ^{integration} of new individuals. This is particularly important in view of the fact that stress can impact the behaviour, cognition, reproductive performance and health of individuals (Costa et al., 2016; Gaillard et al., 2014; Proudfoot and Habing, 2015). It would also be preferable to transfer juvenile individuals aged around 3yo with an adult, and avoid transferring juveniles under one year of age. This would be the best way to decrease the stress of juveniles to a minimum during transfer. On the other hand, forming stable pairs of individuals before and during transfers may increase food intake and weight gain, particularly in calves (Costa et al., 2015). This study has highlighted some interesting results for the improvement of livestock welfare, but other factors could be studied to further enhance animal wellbeing during changes in group composition, notably the personality of the individuals chosen for transfer (Pruitt and Keiser, 2014; Wolf and Weissing, 2012).

Acknowledgements

We would like to thank Cécile Bayeur and Jean-Claude Bieber from the “Parc Naturel des Vosges du Nord”, France and Frédéric Lonchampt from Strasbourg, France for granting us access to the Highland cattle. Our thanks to Arthur Letzelter and Fabien Kauffer for their help obtaining data for the socio-demographic factors of animals, and to Louise Frey and Audrey Claus for their help in data scoring. We thank Joanna Lignot (Munro Language Services) for English editing. Sebastian Sosa and Peng Zhang are funded by the National Natural Science Foundation of China (31470456).

References

- Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, A.M., Fischer, J., 2016. Motivational shifts in aging monkeys and the origins of social selectivity. *Curr. Biol.* 26, 1744–1749.
- Altmann, J., 1974. Observational Study of Behavior: Sampling Methods. *Behaviour* 49, 227–267.
- Balasubramaniam, K.N., Dittmar, K., Berman, C.M., Butovskaya, M., Cooper, M.A., Majolo, B., Ogawa, H., Schino, G., Thierry, B., De Waal, F.B.M., 2012. Hierarchical steepness, counter-aggression, and macaque social style scale. *Am. J. Primatol.* 74, 915–925.
<https://doi.org/10.1002/ajp.22044>
- Banks, D.L., Carley, K.M., 1996. Models for network evolution. *J. Math. Sociol.* 21, 173–196.
- Bartoń, K., 2013. MuMIn: multi-model inference. R Package Version 1.
- Bastian, M., Heymann, S., Jacomy, M., 2009. Gephi: An Open Source Software for Exploring and Manipulating Networks.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. R Package Version 1, 1–23.
- Bøe, K.E., Færevik, G., 2003. Grouping and social preferences in calves, heifers and cows. *Appl. Anim. Behav. Sci.* 80, 175–190.
- Bonacich, P., 2007. Some unique properties of eigenvector centrality. *Soc. Netw.* 29, 555–564.
<https://doi.org/10.1016/j.socnet.2007.04.002>
- Borgeaud, C., Sosa, S., Bshary, R., Sueur, C., van de Waal, E., 2016. Intergroup Variation of Social Relationships in Wild Vervet Monkeys: A Dynamic Network Approach. *Front. Psychol.* 7, 915.
<https://doi.org/10.3389/fpsyg.2016.00915>
- Borgeaud, C., Sosa, S., Sueur, C., Bshary, R., 2017. The influence of demographic variation on social network stability in wild vervet monkeys. *Anim. Behav.* 134, 155–165.
<https://doi.org/10.1016/j.anbehav.2017.09.028>
- Boucherie, P.H., Sosa, S., Pasquaretta, C., Dufour, V., 2017. A longitudinal network analysis of social dynamics in rooks *corvus frugilegus*: repeated group modifications do not affect social network in captive rooks. *Curr. Zool.* 63, 379–388. <https://doi.org/10.1093/cz/zow083>
- Bouissou, M., Boissy, A., 2005. Le comportement social des bovins et ses conséquences en élevage. *INRA Prod. Anim.* 18, 87–99.
- Bouissou, M.F., 1983. Androgens, aggressive behaviour and social relationships in higher mammals. *Horm. Res.* 18, 43–61.
- Bouissou, M.-F., Boissy, A., Le Neindre, P., Veissier, I., 2001. The social behaviour of cattle. *Soc. Behav. Farm Anim.* 113–145.
- Bousquet, C.A.H., Ahr, N., Sueur, C., Petit, O., 2017. Determinants of leadership in groups of female mallards. <https://doi.org/10.1163/1568539X-00003431>
- Boyland, N.K., Mlynski, D.T., James, R., Brent, L.J.N., Croft, D.P., 2016. The social network structure of a dynamic group of dairy cows: From individual to group level patterns. *Appl. Anim. Behav. Sci.* 174, 1–10. <https://doi.org/10.1016/j.applanim.2015.11.016>
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference understanding AIC and BIC in model selection. *Sociol. Methods Res.* 33, 261–304.
- Butt, B., Shortridge, A., WinklerPrins, A.M., 2009. Pastoral herd management, drought coping strategies, and cattle mobility in southern Kenya. *Ann. Assoc. Am. Geogr.* 99, 309–334.
- Costa, J., Meagher, R., von Keyserlingk, M., Weary, D., 2015. Early pair housing increases solid feed intake and weight gains in dairy calves. *J. Dairy Sci.* 98, 6381–6386.
- Costa, J., von Keyserlingk, M., Weary, D., 2016. Invited review: Effects of group housing of dairy calves on behavior, cognition, performance, and health. *J. Dairy Sci.* 99, 2453–2467.
- Crockford, C., 2016. Aging: Lessons for Elderly People from Monkeys. *Curr. Biol.* 26, R532–R534.
- Croft, D.P., James, R., Krause, J., 2008. Exploring Animal Social Networks. Princeton University Press.
- Croft, D.P., Madden, J.R., Franks, D.W., James, R., 2011. Hypothesis testing in animal social networks. *Trends Ecol. Evol.* 26, 502–507. <https://doi.org/10.1016/j.tree.2011.05.012>

- de Vries, H., Stevens, J.M.G., Vervaecke, H., 2006. Measuring and testing the steepness of dominance hierarchies. *Anim. Behav.* 71, 585–592. <https://doi.org/10.1016/j.anbehav.2005.05.015>
- Delville, Y., Mansour, K.M., Ferris, C.F., 1996. Testosterone facilitates aggression by modulating vasopressin receptors in the hypothalamus. *Physiol. Behav.* 60, 25–29.
- Dufour, V., Sueur, C., Whiten, A., Buchanan-Smith, H. m., 2011. The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *Am. J. Primatol.* 73, 802–811. <https://doi.org/10.1002/ajp.20943>
- Estevez, I., Andersen, I.-L., Nævdal, E., 2007. Group size, density and social dynamics in farm animals. *Appl. Anim. Behav. Sci.* 103, 185–204.
- Færevik, G., Jensen, M.B., Bøe, K.E., 2006. Dairy calves social preferences and the significance of a companion animal during separation from the group. *Appl. Anim. Behav. Sci.* 99, 205–221.
- Farine, D.R., 2013. Animal social network inference and permutations for ecologists in R using asnipe. *Methods Ecol. Evol.* 4, 1187–1194. <https://doi.org/10.1111/2041-210X.12121>
- Farine, D.R., n.d. A guide to null models for animal social network analysis. *Methods Ecol. Evol.* n/a-n/a. <https://doi.org/10.1111/2041-210X.12772>
- Farine, D.R., Whitehead, H., 2015. Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* 84, 1144–1163.
- Fox, J., Friendly, G.G., Graves, S., Heiberger, R., Monette, G., Nilsson, H., Ripley, B., Weisberg, S., Fox, M.J., Suggests, M., 2007. The car package.
- Franks, D.W., Ruxton, G.D., James, R., 2010. Sampling animal association networks with the gambit of the group. *Behav. Ecol. Sociobiol.* 64, 493–503. <https://doi.org/10.1007/s00265-009-0865-8>
- Gaillard, C., Meagher, R.K., von Keyserlingk, M.A., Weary, D.M., 2014. Social housing improves dairy calves' performance in two cognitive tests. *PloS One* 9, e90205.
- Gammell, M.P., Vries, H. de, Jennings, D.J., Carlin, C.M., Hayden, T.J., 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index [WWW Document]. *Anim. Behav.* URL <http://dspace.library.uu.nl/handle/1874/17476> (accessed 2.18.17).
- Génot, J.-C., 2000. Conservation de la nature: gérer les espèces ou les habitats? Le cas du parc naturel régional des Vosges du Nord, réserve de la biosphère. *Courr. Environ. INRA* 5–18.
- Gerard, J.-F., Richard-Hansen, C., 1992. Social affinities as the basis of the social organization of a Pyrenean chamois (*Rupicapra pyrenaica*) population in an open mountain range. *Behav. Processes* 28, 111–122.
- Guilhem, C., Bideau, E., Gerard, J., Maublanc, M., 2000. Agonistic and proximity patterns in enclosed mouflon (*Ovis gmelini*) ewes in relation to age, reproductive status and kinship. *Behav. Processes* 50, 101–112.
- Guilhem, C., Gerard, J., Bideau, E., 2002. Rank acquisition through birth order in mouflon sheep (*Ovis gmelini*) ewes. *Ethology* 108, 63–73.
- Gupta, S., Earley, B., Nolan, M., Formentin, E., Crowe, M.A., 2008. Effect of repeated regrouping and relocation on behaviour of steers. *Appl. Anim. Behav. Sci.* 110, 229–243.
- Gutmann, A.K., Špinková, M., Winckler, C., 2015. Long-term familiarity creates preferred social partners in dairy cows. *Appl. Anim. Behav. Sci.* 169, 1–8.
- Hagen, K., Broom, D.M., 2003. Cattle discriminate between individual familiar herd members in a learning experiment. *Appl. Anim. Behav. Sci.* 82, 13–28.
- Hansen, H., McDonald, D.B., Groves, P., Maier, J.A.K., Ben-David, M., 2009. Social Networks and the Formation and Maintenance of River Otter Groups. *Ethology* 115, 384–396. <https://doi.org/10.1111/j.1439-0310.2009.01624.x>
- Heathcote, R.J.P., Darden, S.K., Franks, D.W., Ramnarine, I.W., Croft, D.P., 2017. Fear of predation drives stable and differentiated social relationships in guppies. *Sci. Rep.* 7, 41679. <https://doi.org/10.1038/srep41679>
- Kasper, C., Voelkl, B., 2009. A social network analysis of primate groups. *Primates* 50, 343–356. <https://doi.org/10.1007/s10329-009-0153-2>
- Kimura, R., 1998. Mutual grooming and preferred associate relationships in a band of free-ranging horses. *Appl. Anim. Behav. Sci.* 59, 265–276.

- Koene, P., Ipema, B., 2014. Social Networks and Welfare in Future Animal Management. *Animals* 4, 93–118. <https://doi.org/10.3390/ani4010093>
- Kondo, S., Sekine, J., Okubo, M., Asahida, Y., 1989. The effect of group size and space allowance on the agonistic and spacing behavior of cattle. *Appl. Anim. Behav. Sci.* 24, 127–135.
- Kurvers, R.H., Adamczyk, V.M., Kraus, R.H., Hoffman, J.I., van Wieren, S.E., van der Jeugd, H.P., Amos, W., Prins, H.H., Jonker, R.M., 2013. Contrasting context dependence of familiarity and kinship in animal social networks. *Anim. Behav.* 86, 993–1001.
- Laforge, M.P., Michel, N.L., Wheeler, A.L., Brook, R.K., 2016. Habitat selection by female moose in the Canadian prairie ecozone. *J. Wildl. Manag.* 80, 1059–1068.
- Le Pendu, Y., Guilhem, C., Briedermann, L., Maublanc, M.-L., Gerard, J.-F., 2000. Interactions and associations between age and sex classes in mouflon sheep (*Ovis gmelini*) during winter. *Behav. Processes* 52, 97–107.
- Levé, M., Sueur, C., Petit, O., Matsuzawa, T., Hirata, S., 2016. Social grooming network in captive chimpanzees: does the wild or captive origin of group members affect sociality? *Primates* 57, 73–82.
- Lopes, L.B., Eckstein, C., Pina, D.S., Carnevalli, R.A., 2016. The influence of trees on the thermal environment and behaviour of grazing heifers in Brazilian Midwest. *Trop. Anim. Health Prod.* 48, 755–761.
- Lusseau, D., Newman, M.E.J., 2004. Identifying the role that animals play in their social networks. *Proc. R. Soc. B Biol. Sci.* 271, S477–S481. <https://doi.org/10.1098/rsbl.2004.0225>
- Massen, J.J., Koski, S.E., 2014. Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. *Evol. Hum. Behav.* 35, 1–8.
- McCann, N.P., Moen, R.A., Windels, S.K., Harris, T.R., 2016. Bed sites as thermal refuges for a cold-adapted ungulate in summer. *Wildl. Biol.* 22, 228–237.
- McComb, K., Shannon, G., Durant, S.M., Sayialel, K., Slotow, R., Poole, J., Moss, C., 2011. Leadership in Elephants: The Adaptive Value of Age. *Proc. R. Soc. B Biol. Sci.* <https://doi.org/10.1098/rspb.2011.0168>
- McPherson, M., Smith-Lovin, L., Cook, J.M., 2001. Birds of a feather: Homophily in social networks. *Annu. Rev. Sociol.* 27, 415–444.
- Muller, S., Dutoit, T., Alard, D., Grevilliot, F., 1998. Restoration and Rehabilitation of Species-Rich Grassland Ecosystems in France: a Review. *Restor. Ecol.* 6, 94–101.
- Pasquaretta, C., Klenschi, E., Pansanel, J., Battesti, M., Mery, F., Sueur, C., 2016. Understanding Dynamics of Information Transmission in *Drosophila melanogaster* Using a Statistical Modeling Framework for Longitudinal Network Data (the RSiena Package). *Front. Psychol.* 7. <https://doi.org/10.3389/fpsyg.2016.00539>
- Patison, K.P., Swain, D.L., Bishop-Hurley, G.J., Robins, G., Pattison, P., Reid, D.J., 2010. Changes in temporal and spatial associations between pairs of cattle during the process of familiarisation. *Appl. Anim. Behav. Sci.* 128, 10–17.
- Pinter-Wollman, N., Hobson, E.A., Smith, J.E., Edelman, A.J., Shizuka, D., Silva, S. de, Waters, J.S., Prager, S.D., Sasaki, T., Wittemyer, G., Fewell, J., McDonald, D.B., 2013. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav. Ecol.* art047. <https://doi.org/10.1093/beheco/art047>
- Pourhoseingholi, M.A., Baghestani, A.R., Vahedi, M., 2012. How to control confounding effects by statistical analysis. *Gastroenterol. Hepatol. Bed Bench* 5, 79–83.
- Proudfoot, K., Habing, G., 2015. Social stress as a cause of diseases in farm animals: current knowledge and future directions. *Vet. J.* 206, 15–21.
- Pruitt, J.N., Keiser, C.N., 2014. The personality types of key catalytic individuals shape colonies' collective behaviour and success. *Anim. Behav.* 93, 87–95.
- R Development Core Team, 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raussi, S., Niskanen, S., Siivonen, J., Hänninen, L., Hepola, H., Jauhiainen, L., Veissier, I., 2010. The formation of preferential relationships at early age in cattle. *Behav. Processes* 84, 726–731.

- Reinhardt, V., Reinhardt, A., 1981. Cohesive Relationships in a Cattle Herd (*Bos Indicus*). *Behaviour* 77, 121–150. <https://doi.org/10.1163/156853981X00194>
- Righi, S., Takacs, K., 2014. Triadic balance and closure as drivers of the evolution of cooperation. Presented at the Social Simulation Conference.
- Roberts, J.M., Browning, B.A., 1998. Proximity and threats in highland ponies. *Soc. Netw.* 20, 227–238.
- Ruckstuhl, K.E., Neuhaus, P., 2000. Sexual Segregation in Ungulates: A New Approach. *Behaviour* 137, 361–377.
- Šárová, R., Špinka, M., Stěhulová, I., Ceacero, F., Šimečková, M., Kotrba, R., 2013. Pay respect to the elders: age, more than body mass, determines dominance in female beef cattle. *Anim. Behav.* 86, 1315–1323. <https://doi.org/10.1016/j.anbehav.2013.10.002>
- Sato, S., Tarumizu, K., Hatae, K., 1993. The influence of social factors on allogrooming in cows. *Appl. Anim. Behav. Sci.* 38, 235–244.
- Schein, M.W., Fohrman, M.H., 1955. Social dominance relationships in a herd of dairy cattle. *Br. J. Anim. Behav.* 3, 45–55. [https://doi.org/10.1016/S0950-5601\(55\)80012-3](https://doi.org/10.1016/S0950-5601(55)80012-3)
- Shimada, M., Sueur, C., 2014. The importance of social play network for infant or juvenile wild chimpanzees at Mahale Mountains National Park, Tanzania. *Am. J. Primatol.* n/a-n/a. <https://doi.org/10.1002/ajp.22289>
- Snijders, L., Blumstein, D.T., Stanley, C.R., Franks, D.W., 2017. Animal Social Network Theory Can Help Wildlife Conservation. *Trends Ecol. Evol.* 32, 567–577. <https://doi.org/10.1016/j.tree.2017.05.005>
- Sosa, S., 2016. The Influence of Gender, Age, Matriline and Hierarchical Rank on Individual Social Position, Role and Interactional Patterns in *Macaca sylvanus* at ‘La Forêt des Singes’: A Multilevel Social Network Approach. *Front. Psychol.* 7.
- Sueur, C., Jacobs, A., Amblard, F., Petit, O., King, A.J., 2011a. How can social network analysis improve the study of primate behavior? *Am. J. Primatol.* 73, 703–719.
- Sueur, C., King, A.J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C.M., Williams, L., Zinner, D., Aureli, F., 2011b. Collective decision-making and fission–fusion dynamics: a conceptual framework. *Oikos* 120, 1608–1617. <https://doi.org/10.1111/j.1600-0706.2011.19685.x>
- Sueur, C., Kuntz, C., Debergue, E., Keller, B., Robic, F., Siegwalt-Baudin, F., Richer, C., Ramos, A., Pelé, M., 2017. Leadership linked to group composition in Highland cattle (*Bos taurus*): Implications for livestock management. *Appl. Anim. Behav. Sci.* <https://doi.org/10.1016/j.applanim.2017.09.014>
- Sueur, C., Pelé, M., 2015. Utilisation de l’analyse des réseaux sociaux dans la gestion des animaux maintenus en captivité, in: *Analyse Des Réseaux Sociaux Appliquée à l’Ethologie et à l’Ecologie*. Editions Matériologiques, pp. 445–468.
- Syme, L.A., Syme, G., Waite, T., Pearson, A., 1975. Spatial distribution and social status in a small herd of dairy cows. *Anim. Behav.* 23, 609–614.
- Takeda, K., Sato, S., Sugawara, K., 2003. Familiarity and group size affect emotional stress in Japanese Black heifers. *Appl. Anim. Behav. Sci.* 82, 1–11.
- Tokuyama, N., Furuichi, T., 2017. Leadership of old females in collective departures in wild bonobos (*Pan paniscus*) at Wamba. *Behav. Ecol. Sociobiol.* 71, 55. <https://doi.org/10.1007/s00265-017-2277-5>
- VILLARET, J.-C., BON, R., 1998. Sociality and relationships in Alpine ibex (*Capra ibex*).
- Von Keyserlingk, M., Olenick, D., Weary, D., 2008. Acute behavioral effects of regrouping dairy cows. *J. Dairy Sci.* 91, 1011–1016.
- Whitehead, H., 2009. SOCPROG programs: analysing animal social structures. *Behav. Ecol. Sociobiol.* 63, 765–778. <https://doi.org/10.1007/s00265-008-0697-y>
- Wilson, A.D.M., Krause, S., Ramnarine, I.W., Borner, K.K., Clément, R.J.G., Kurvers, R.H.J.M., Krause, J., 2015. Social networks in changing environments. *Behav. Ecol. Sociobiol.* 1–13. <https://doi.org/10.1007/s00265-015-1973-2>

- Winfield, C., Syme, G., Pearson, A., 1981. Effect of familiarity with each other and breed on the spatial behaviour of sheep in an open field. *Appl. Anim. Ethol.* 7, 67–75.
- Wintz, M., Fabien, D., 2012. La perception des friches dans les Vosges du nord: entre nature abandonnée et nature «déjà là». *Ann. Sci. Réserve Biosph. Transfront.*
- Wolf, M., Weissing, F.J., 2012. Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.* 27, 452–461. <https://doi.org/10.1016/j.tree.2012.05.001>
- Wrangham, R.W., 1980. An Ecological Model of Female-Bonded Primate Groups. *Behaviour* 75, 262–300.

Table legends

Table 1: Characteristics of the four Highland cattle group sites.

Observation site	GPS coordinates	Area (m ²)	Observation time	Number of changes in group composition
Robertsau (Rob)	48.611237, 7.806514	5 enclosure changes: 66 438;32 801; 44 028;80 501;33 637; 44 028	14/04/15- 28/08/15, 22/01/16- 29/04/16	2
Niedersteinbach (Nie)	49.029522, 7.720504	86 787	14/04/15- 28/08/15	1
Sturzelbronn (Stu)	49.057404, 7.580153	112 273	14/04/15- 28/08/15	2
Rolbing (Rol)	49.10545, 7.26120	71 454	22/01/16- 29/04/16	None

Table 2: Group size, number of scans and observation days, number of agonistic interactions, sex ratio and age ratio for each group composition (including changes in enclosure). For sex ratio, M= Male and F=Female. CM indicates castrated males. For age ratio, A=Adult and J=Juvenile (≤ 2 yo).

Group composition	Number of scans (and days)	Number of agonistic interactions	Group size	Sex ratio	Age ratio
Niedersteinbach 1	429 (7)	150	10	1 M - 9 F	9 A - 1 J
Niedersteinbach 2	922 (13)	74	9	9 F	8 A - 1 J
Robertsau 1	207 (6)	214	14	14 F	9 A - 5 J
Robertsau 2	211 (7)	369	21	21 F	9 A - 5 J
Robertsau 3	118 (4)	278	21	21 F	9 A - 5 J
Robertsau 4	221 (7)	557	21	21 F	9 A - 5 J
Robertsau 5	174 (4)	104	12	12 F	4 A - 8 J
Robertsau 6	321 (6)	233	12	12 F	4 A - 8 J
Robertsau 7	272 (4)	99	12	12 F	4 A - 8 J

Rolbing	416 (9)	74	11	7 M - 2 CM - 2 F	2 A - 9 J
Sturzelbronn 1	172 (4)	83	18	3 M - 15 F	8 A - 10 J
Sturzelbronn 2	133 (2)	48	8	8 F	8 A
Sturzelbronn 3	899 (13)	266	9	1 M - 8 F	1 A - 8 A

Table 3: Correlations of dyadic associations matrices with matrices of characteristic differences (age, dominance and sex). The last column also indicates the tests between matrices for age difference and dominance difference. NA = Non-Applicable, due to the presence of just one sex in the group composition. For the global value, POS indicates that most of significant correlations were positive; NEG indicates that most of significant correlations were negative.

Group composition	DyaAsso-Dominance	DyaAsso-Sex	DyaAsso-Age	Dominance-Age
Niedersteinbach 1	p = 0.332 (r = 0.06)	p = 1 (r = -0.15)	p = 0.039 (r = 0.16)	p = 0.007 (r = 0.43)
Niedersteinbach 2	p = 0.302 (r = 0.10)	NA (just one sex)	p = 0.431 (r = -0.01)	p = 0.448 (r = 0.08)
Robertsau 1	p = 0.036 (r = -0.29)	NA (just one sex)	p = 0.004 (r = -0.15)	p = 0.002 (r = 0.52)
Robertsau 2	p<0.001 (r = -0.40)	NA (just one sex)	p<0.001 (r = -0.32)	p<0.001 (r = 0.63)
Robertsau 3	p<0.001 (r = -0.21)	NA (just one sex)	p = 0.001 (r = -0.19)	p<0.001 (r = 0.55)
Robertsau 4	p<0.001 (r = -0.40)	NA (just one sex)	p<0.001 (r = -0.32)	p<0.001 (r = 0.70)
Robertsau 5	p = 0.001 (r = -0.35)	NA (just one sex)	p = 0.008 (r = -0.25)	p = 0.042 (r = 0.28)
Robertsau 6	p<0.001 (r = -0.43)	NA (just one sex)	p = 0.009 (r = -0.23)	p = 0.036 (r = 0.28)
Robertsau 7	p = 0.004 (r = -0.30)	NA (just one sex)	p = 0.006 (r = -0.24)	p = 0.013 (r = 0.39)
Rolbing	p = 0.015 (r = -0.30)	p = 0.006 (r = 0.31)	p<0.001 (r = -0.36)	p = 0.035 (r = 0.43)

Sturzelbronn 1	p =0.028 (r = -0.13)	p = 0.168 (r = 0.05)	p = 0.948 (r = -0.10)	p<0.001 (r = 0.63)
Sturzelbronn 2	p =0.592 (r = -0.03)	NA (just one sex)	p = 0.262 (r = 0.10)	p = 0.046 (r = 0.34)
Sturzelbronn 3	p =0.006 (r = -0.42)		p = 1 (r = -0.16)	p = 0.708 (r = -0.03)
Global	p = 1.019e-13	p = 0.087	p = 7.728e-12	p = 2.584e-23
	NEG (r = 0.26)	POS(r = 0.17)	NEG(r = 0.19)	POS(r = 0.41)

Table 4: Values of the variables retained in the best models to explain the variance of the eigenvector centrality.

	Estimate	Std.Error	z value	PPerm left side	PPerm right side
(Intercept)	0.388	0.0157	24.571	0.00	1.00
Dominance	-0.051	0.0204	2.463	0.199	0.801
Familiarity	-0.029	0.026	1.105	0.298	0.702
Age	0.004	0.002	1.531	0.664	0.336

Table 5: Values of the variables retained in the best models to explain the variance of the strength of associations.

	Estimate	Std.Error	z value	Pperm left side	PPerm right side
(Intercept)	0.915	0.138	6.578	0.65	0.35
Familiarity	0.259	0.065	3.94	1.00	0.00
SexF	-0.301	0.161	1.83	0.003	0.997
SexM	-0.156	0.141	1.09	0.175	0.825
Age	0.001	0.005	0.341	0.98	0.02
Dominance	-0.004	0.19	0.211	0.357	0.643

Table 6: Values of the variables retained in the best models to explain the variance of the difference of eigenvector centrality after transfer.

	Estimate	Std.Error	z value	Pperm left side	Pperm right side
(Intercept)	-0.010	0.016	0.629	0.344	0.656
Age	0.009	0.003	2.38	0.985	0.015
Familiarity	-0.018	0.548	0.33	0.438	0.562
Dominance	0.017	0.042	0.392	0.398	0.602

Table 7: Values of the variables retained in the best models to explain the variance of the difference of strength of associations after transfer.

	Estimate	Std.Error	Adjusted SE	z value	Pperm left side	Pperm right side
(Intercept)	-0.730	0.145	0.147	4.975	0.00	1.00
Dominance	0.120	0.143	0.144	0.831	0.90	0.10
Familiarity	0.816	0.151	0.153	5.323	1.00	0.00
Age	0.001	0.005	0.005	0.213	0.812	0.188
N	-0.0003	0.002	0.002	0.159	0.112	0.888

Figure legends

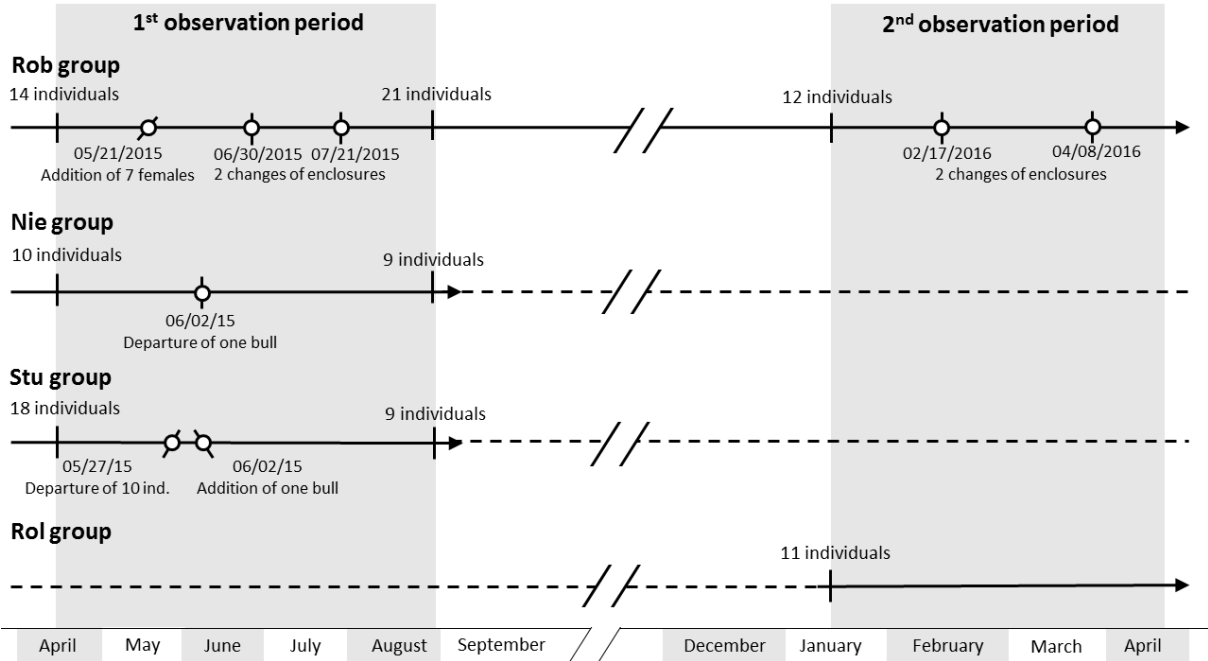


Figure 1: Chronological scheme of the composition changes in all four groups. Solid lines indicate the period of observation, whilst dotted lines indicate an absence of observation. Red dots indicate changes in group composition or enclosure.

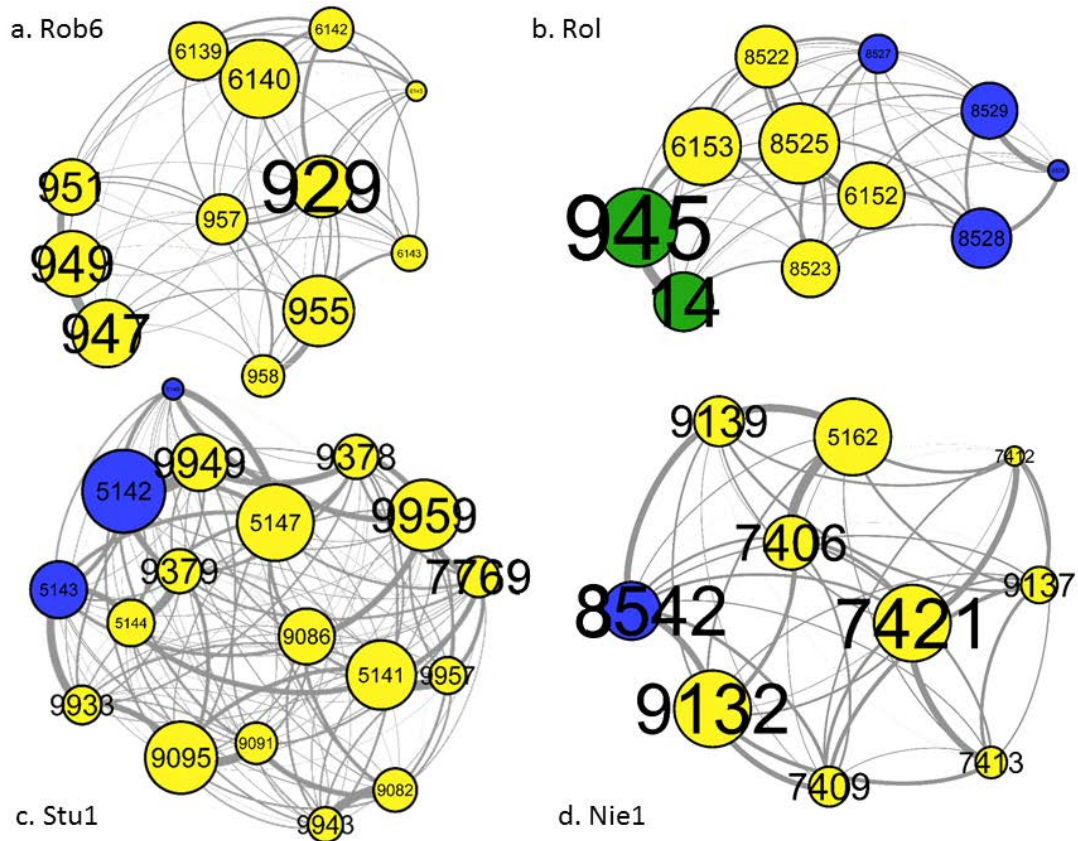


Figure 2: Instances of four group compositions. a. Robertsau 6 (321 scans, six days of observation), b. Rolbing (416 scans, nine days of observation), c. Sturzelbronn1 (172 scans, four days of observation), d. Niedersteinbach1 (429 scans, seven days of observation). One node represents one individual, each identified by a number (label). The links between nodes are dyadic associations. The size of nodes depends on the strength of associations but are relative to each group composition (the strength are not comparable between networks). The thickness of links depend on the weight of dyadic associations. The size of labels increases with the age of individuals. Yellow, blue and green node colours indicate females, males and castrated males, respectively. Individuals are positioned according to their weight of associations: two individuals located close to each other share a stronger dyadic association than distant individuals. Graphs were created using Gephi 0.91 (Bastian et al., 2009) with the ‘force atlas’ spatialization package.

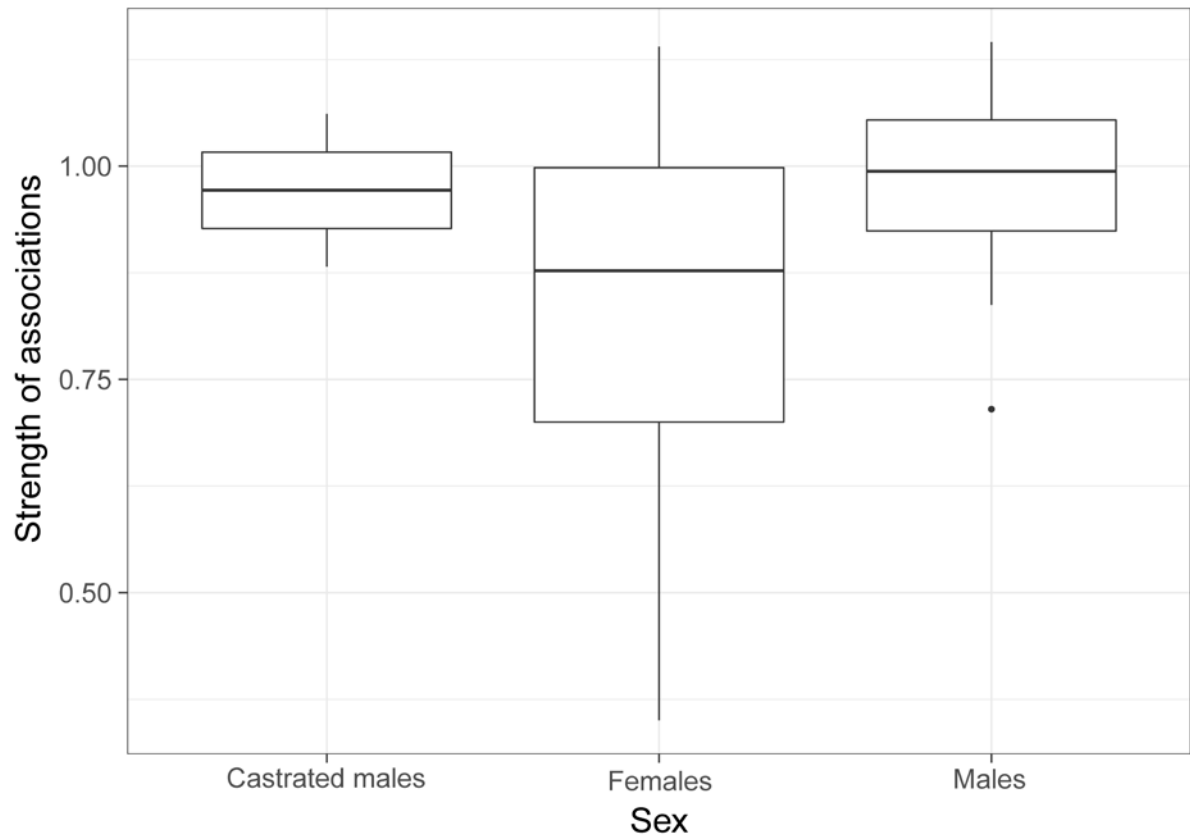


Figure 3: Strength of associations according to familiarity of individuals (i.e., proportion of familiar individuals in the group). GLMM highlighted a significant effect of familiarity on strength of associations.

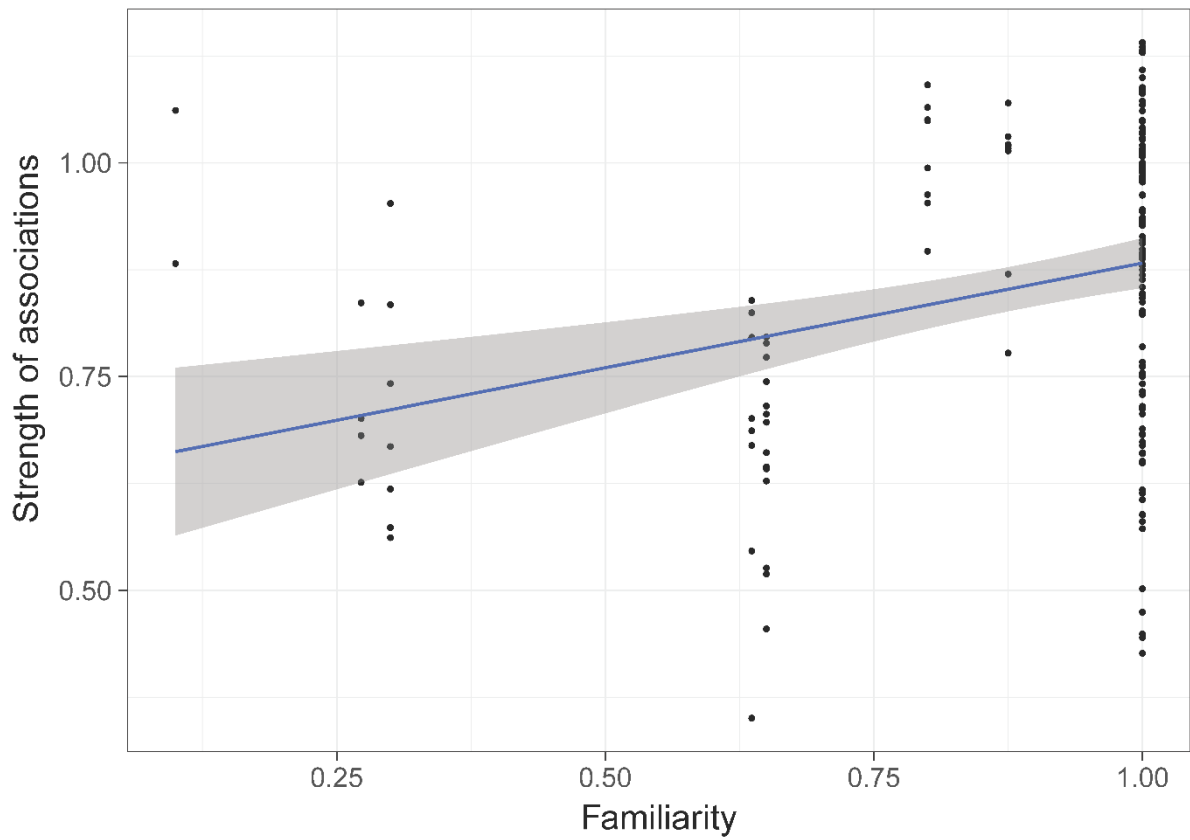


Figure 4: Strength of associations according to the sex of individuals. GLMM reveals that only the strength of associations of castrated males is different to those of females.

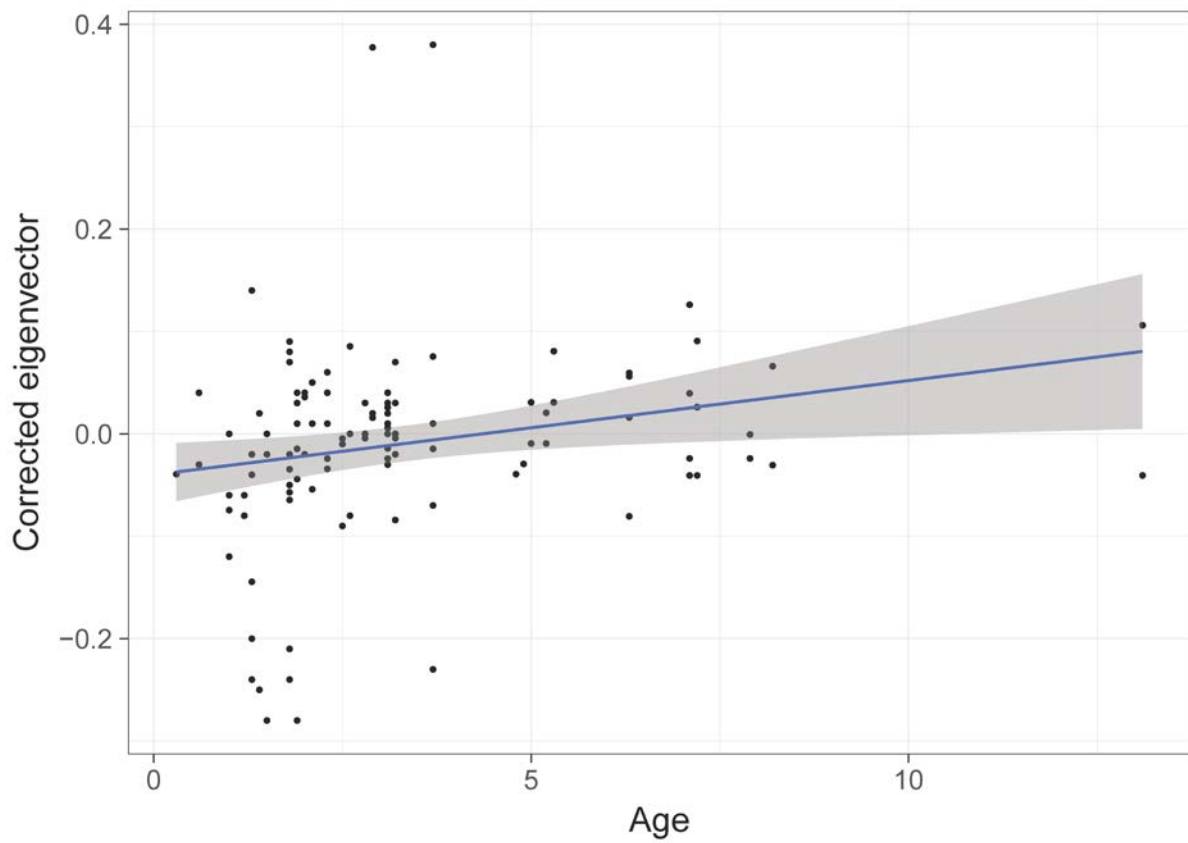


Figure 5: Difference of eigenvectors after a transfer, according to the age of individuals. GLMM highlights a significant effect of age of individuals on the change in strength of associations after a transfer.

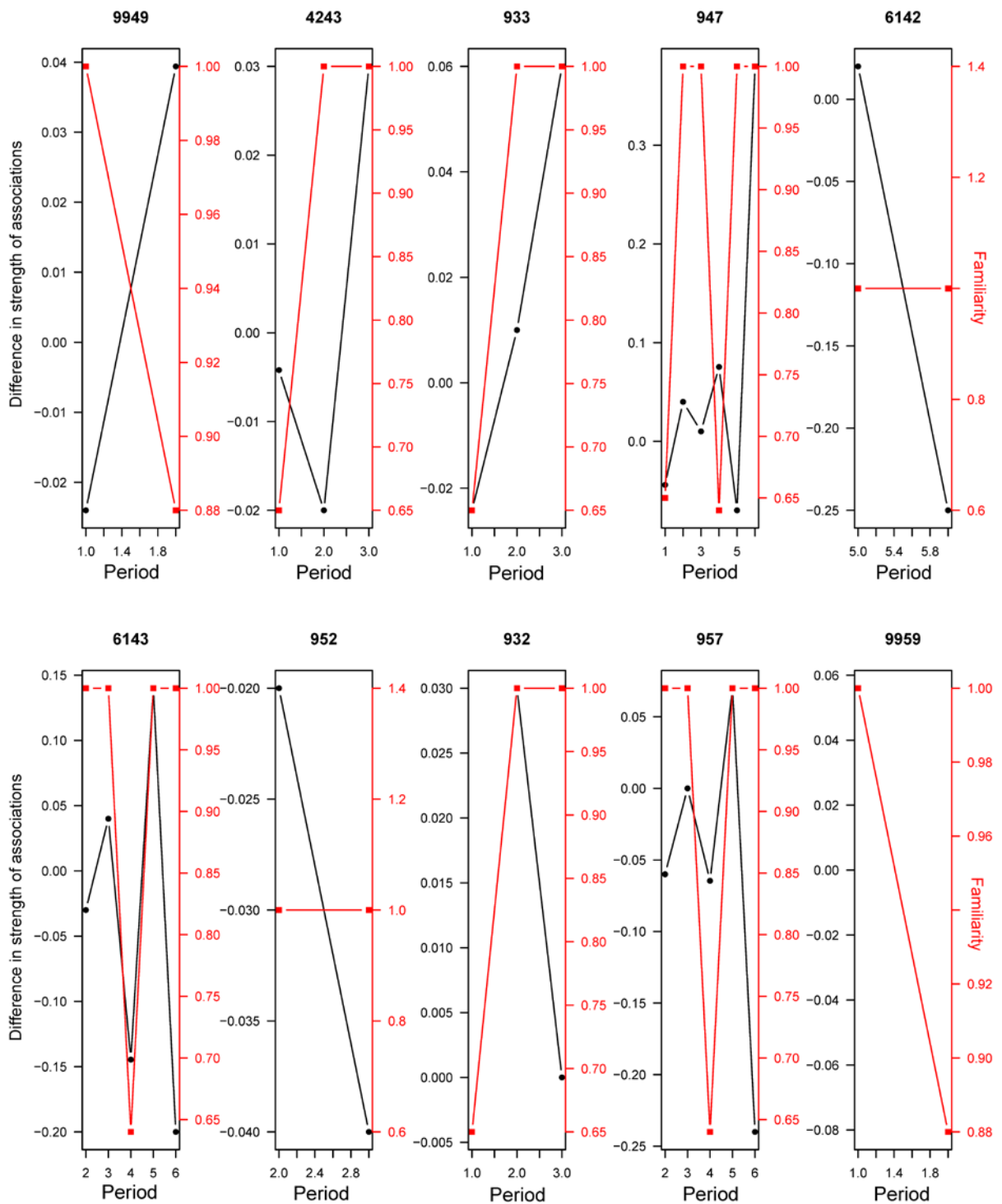


Figure 6: Difference in strength of associations (black line) and familiarity (red line, as proportion of familiar individuals in the group) between different periods of transfer (Periods exclude any transfer activity). Examples for ten individuals chosen randomly.

Supplementary information for :

Impact of group management and transfer on individual sociality in Highland cattle (*Bos Taurus*)

Sebastian Sosa¹, Marie Pelé², Élise Debergue³, Cédric Kuntz³, Blandine Keller³, Florian Robic³, Flora Siegwalt-Baudin³, Camille Richer³, Peng Zhang¹, Amandine Ramos³, Cédric Sueur³

¹ Anthropology Department, Sun-Yat sen University, Guang Zhou, China

² Ethobiosciences, Research and Consultancy Agency in Animal Well-Being and Behaviour, Strasbourg, France

³ Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

Corresponding author: cedric.sueur@iphc.cnrs.fr, 0033(0)88107453, IPHC UMR 7178, 23 rue Becquerel F-67000 Strasbourg, France



Figure S1: locations of the four different sites.

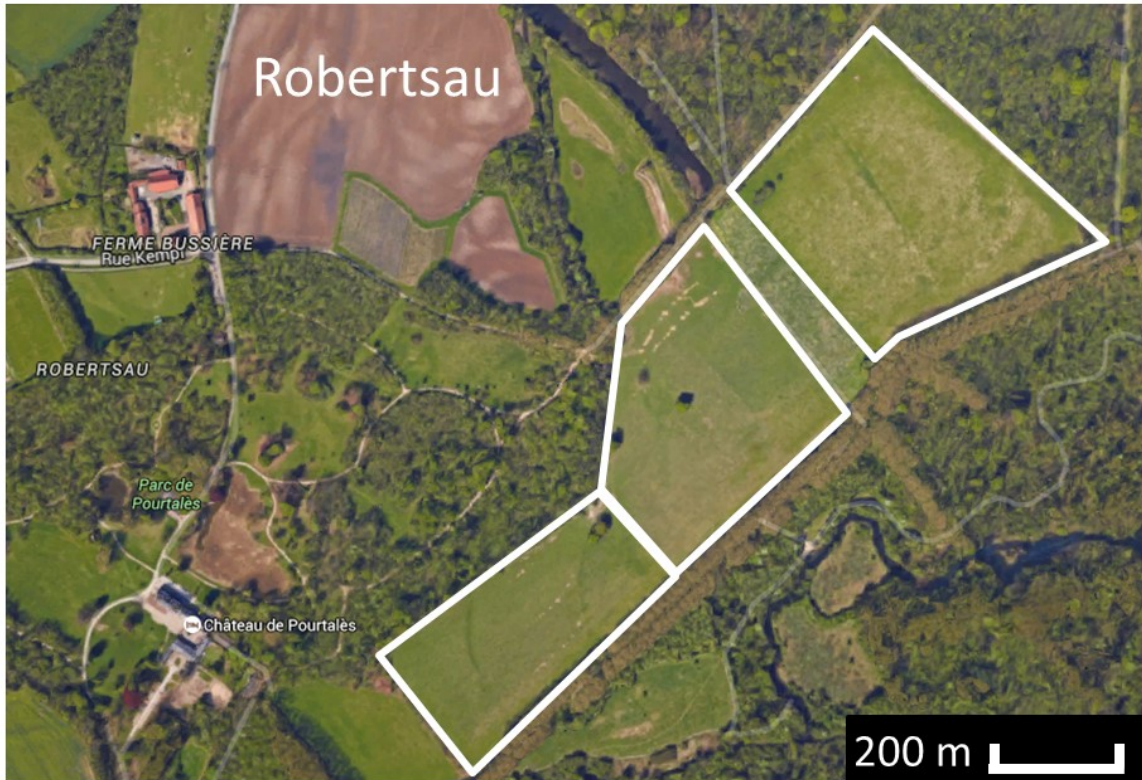


Figure S2: Robertsau study site with the different enclosures



Figure S3: Niedersteinbach study site

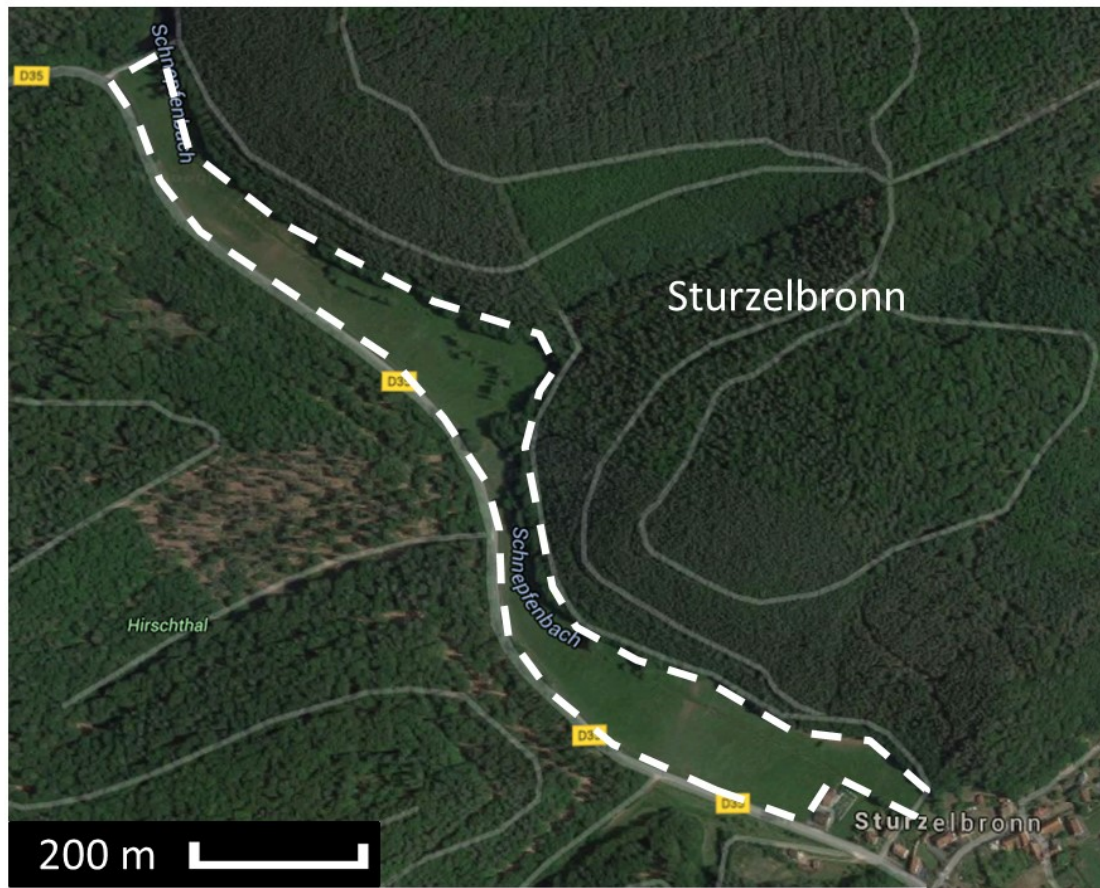
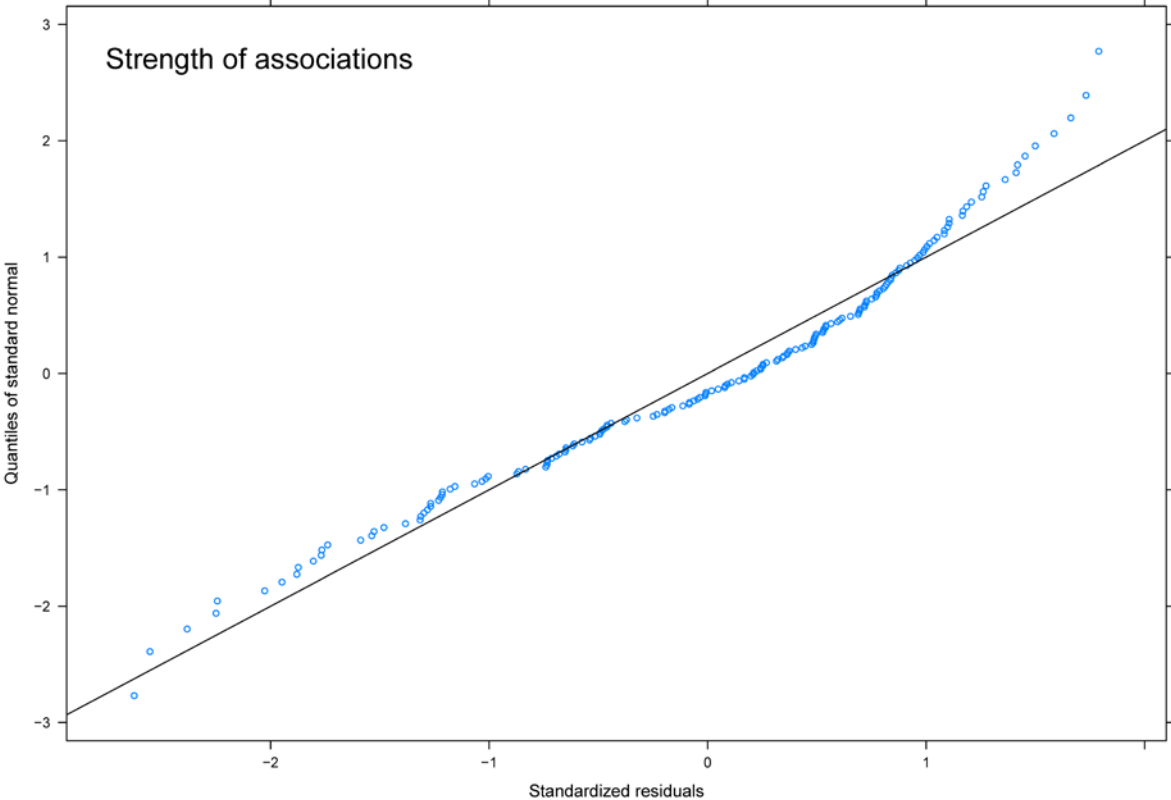
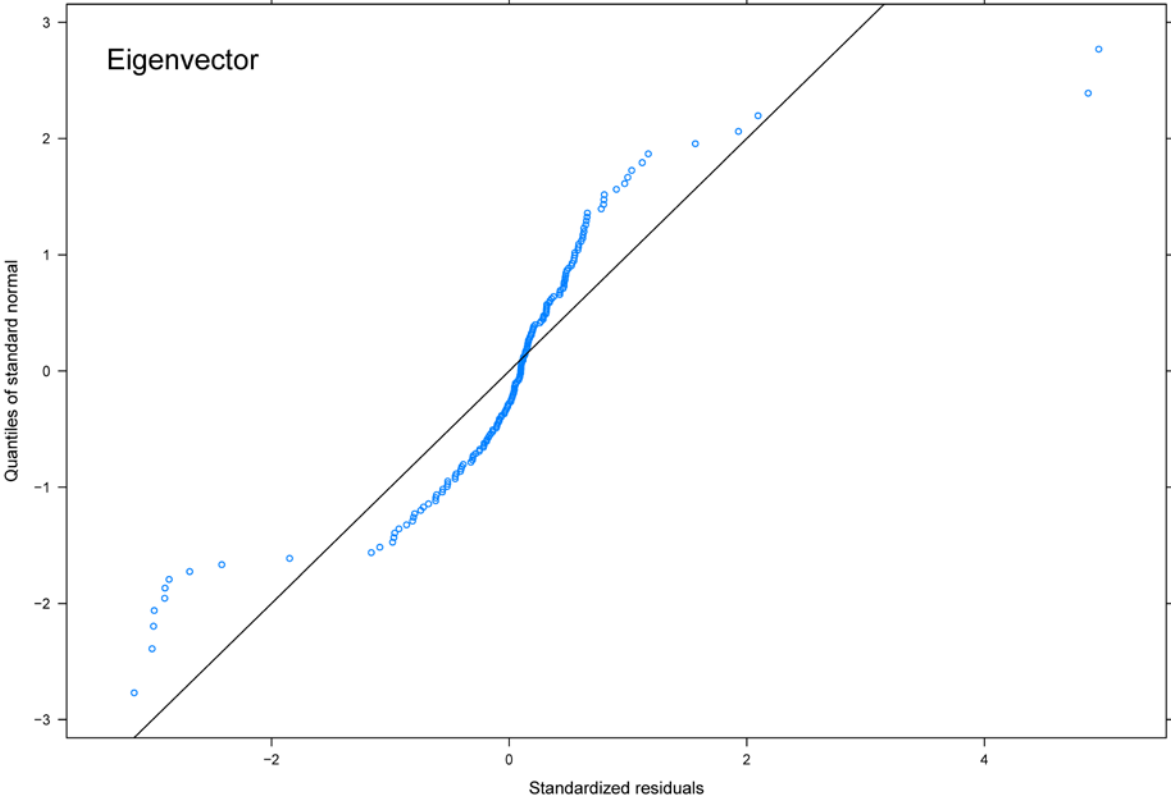


Figure S4: Sturzelbronn study site



Figure S5: Rolbing study site

Table S1: Plots of residual normality distribution



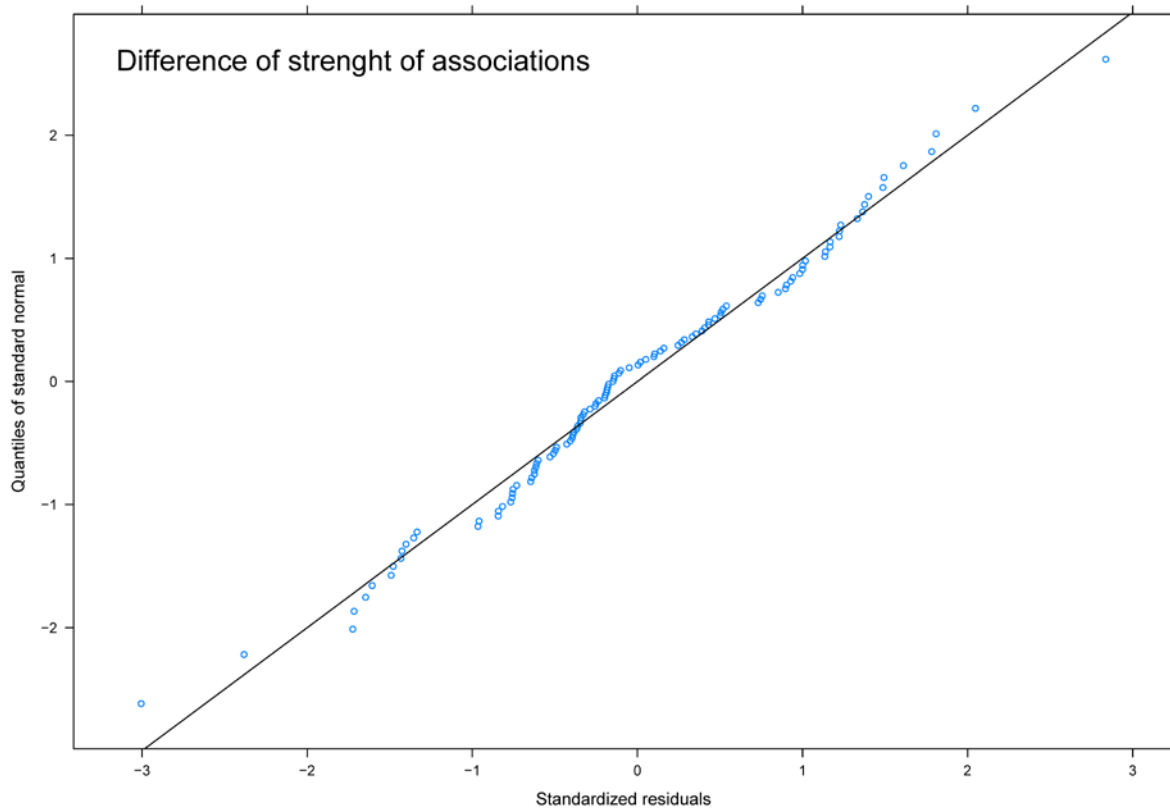
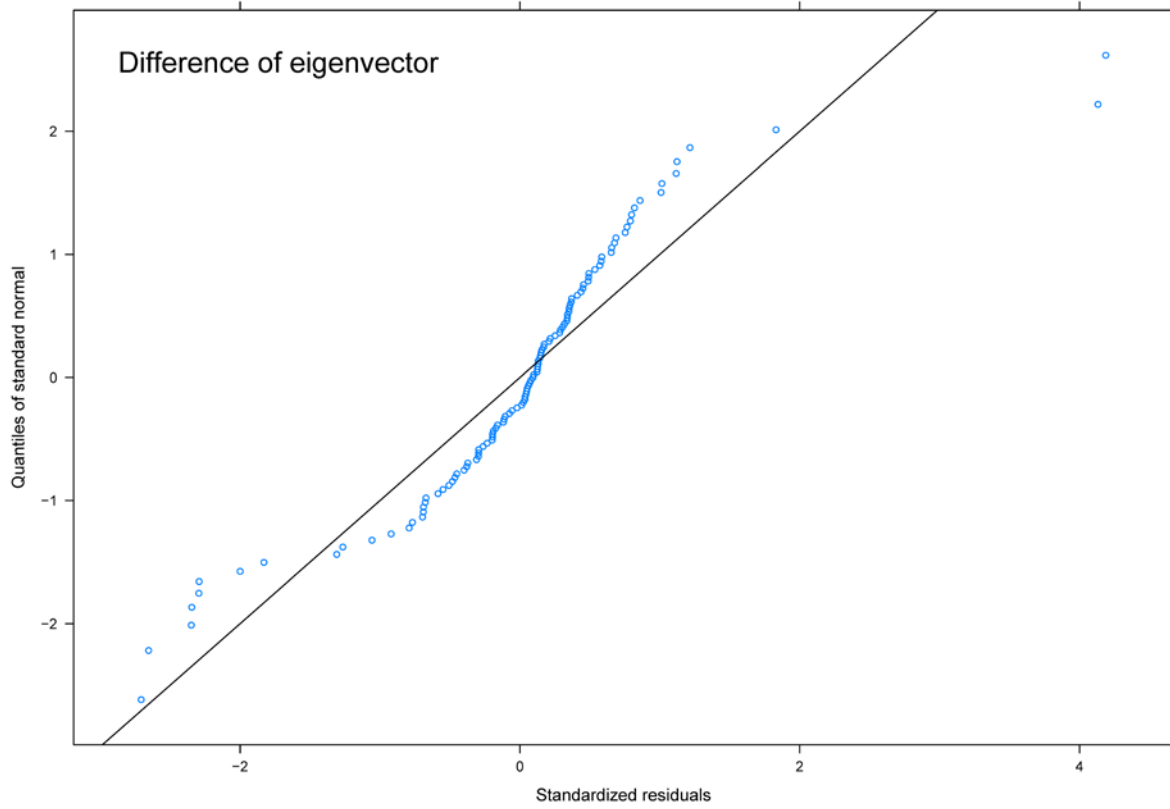


Table S2: Model selection table for the influence of socio-demographic factors on the eigenvector centrality. Models are ranked according to the best AIC

Model n°	(Int)	age	domin	famil	sex	df	logLik	AIC	ΔAIC	weight
13	0.9447			0.2704	+	6	55.8	-99.6	0.0	0.707
14	0.9074	0.0147		0.2465	+	7	55.0	-96	3.7	0.113
5	0.6884	0.1959				4	51.8	-95.5	4.1	0.091
15	0.9531		-0.0583	0.2663	+	7	54.4	-94.7	4.9	0.06
7	0.7191		-0.0580	0.194		5	50.3	-90.6	9.1	0.008
1	0.8599					3	48.2	-90.5	9.2	0.007
16	0.9119	0.0139	-0.0172	0.246	+	8	52.9	-89.8	9.8	0.005
6	0.6651	0.0124		0.1749		5	49.7	-89.4	10.2	0.004
9	0.9718				+	5	48.5	-86.9	12.7	0.001
2	0.808	0.0155				4	47.4	-86.8	12.9	0.001
10	0.9228	0.0181			+	6	49.2	-86.4	13.3	0.001
3	0.8929		-0.0658			4	46.9	-85.8	13.8	0.001
8	0.6824	0.0113	-0.0276	0.1755		6	47.8	-83.5	16.1	0
11	0.9818		-0.0736		+	6	47.4	-82.8	16.8	0
4	0.8254	0.0143	-0.0265			5	45.4	-80.9	18.8	0
12	0.9282	0.0171	-0.0211		+	7	47.2	-80.4	19.3	0

Table S3: Model selection table for the influence of socio-demographic factors on the strength of associations. Models are ranked according to the best AIC

Model n°	(Int)	age	domin	famil	sex	df	logLik	AIC	ΔAIC	weight
13	0.9447			0.2704	+	6	55.82	-99.6	0.0	0.707
14	0.9074	0.0147		0.2465	+	7	54.98	-96	3.7	0.113
5	0.6884			0.1959		4	51.77	-95.5	4.1	0.091
15	0.9531		-0.0583	0.2663	+	7	54.36	-94.7	4.9	0.06
7	0.7191		-0.0580	0.194		5	50.28	-90.6	9.1	0.008
1	0.8599					3	48.23	-90.5	9.2	0.007
16	0.9119	0.0139	-0.0172	0.246	+	8	52.92	-89.8	9.8	0.005
6	0.6651	0.0124		0.1749		5	49.70	-89.4	10.2	0.004
9	0.9718				+	5	48.46	-86.9	12.7	0.001
2	0.808	0.0155				4	47.38	-86.8	12.9	0.001
10	0.9228	0.0181			+	6	49.18	-86.4	13.3	0.001
3	0.8929		-0.0658			4	46.91	-85.8	13.8	0.001
8	0.6824	0.0113	-0.0276	0.1755		6	47.76	-83.5	16.1	0
11	0.9818		-0.0736		+	6	47.42	-82.8	16.8	0
4	0.8254	0.0143	-0.0265			5	45.44	-80.9	18.8	0
12	0.9282	0.0171	-0.0211		+	7	47.19	-80.4	19.3	0

Table S4: Model selection table for the influence of socio-demographic factors on the difference of eigenvector centralities after a transfer. Models are ranked according to the best AIC

Model n°	(Intrc)	age	domin	famil	nb.ind	df	logLik	AIC	ΔAIC	weight
1	-0.0096					3	102.32	-198.6	0.0	0.854
2	-0.0400	0.0092				4	100.56	-193.1	5.5	0.054
5	0.0073			-0.0185		4	100.40	-192.8	5.9	0.046
3	-0.0090		0.0171			4	100.17	-192.3	6.3	0.036
9	-0.0107				-0.0022	4	97.62	-187.2	11.4	0.003
6	-0.0308	0.0091		-0.0099		5	98.57	-187.1	11.5	0.003
7	0.0217		0.0278	-0.0332		5	98.43	-186.9	11.8	0.002
4	-0.0418	0.0096	-0.0146			5	98.41	-186.8	11.8	0.002
13	0.0155			-0.0287	-0.0024	5	95.78	-181.6	17.1	0
8	-0.0396	0.0096	-0.0138	-0.0023		6	96.52	-181	17.6	0
11	-0.0102		0.0111		-0.0021	5	95.43	-180.9	17.8	0
10	-0.0390	0.0088			-0.0008	5	95.39	-180.8	17.9	0
15	0.0275		0.0238	-0.0409	-0.0023	6	93.77	-175.5	23.1	0
14	-0.0255	0.0086		-0.0143	-0.0009	6	93.44	-174.9	23.8	0
12	-0.0408	0.0092	-0.0155		-0.0008	6	93.25	-174.5	24.2	0
16	-0.0340	0.0090	-0.0130	-0.0070	-0.0009	7	91.39	-168.8	29.9	0

Table S5: Model selection table for the influence of socio-demographic factors on the difference of strength of associations after a transfer. Models are ranked according to the best AIC.

Model n°	Int.	Age	Domin	Famil	Nb.ind	df	logLik	AIC	delta	weight
7	-0.6639		0.242	0.7524		5	4.422	1.2	0.0	0.473
5	-0.7887			0.8802		4	3.352	1.3	0.1	0.441
6	-0.8732	0.0203		0.8992		5	1.985	6	4.9	0.041
13	-0.7529			0.8354	-0.0103	5	1.101	7.8	6.6	0.017
15	-0.6394		0.2252	0.7199	-0.0095	6	1.89	8.2	7.1	0.014
8	-0.7600		0.0150	0.1768	0.8009	6	1.884	8.2	7.1	0.014
14	-0.8281	0.0158		0.8619	-0.0076	6	-1.279	14.6	13.4	0.001
16	-0.7085	0.0102	0.1839	0.7581	-0.0079	7	-1.281	16.6	15.4	0
3	0.0318		0.4848			4	-7.173	22.3	21.2	0
11	0.0244		0.4490		-0.0125	5	-8.839	27.7	26.5	0
4	0.0211	0.0031	0.4744			5	-10.745	31.5	30.3	0
1	0.0156					3	-14.542	35.1	33.9	0
12	0.0370	-0.0038	0.4599		-0.0130	6	-12.375	36.8	35.6	0
9	0.0080				-0.0155	4	-15.18	38.4	37.2	0
2	-0.0375	0.0160				4	-17.066	42.1	41.0	0
10	-0.0182	0.0081			-0.0142	5	-18.492	47	45.8	0