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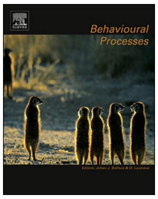

The social network structure of a semi-free roaming European bison herd (*Bison bonasus*)

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ABSTRACT

The use of social network analysis to better understand animal behaviour has led to an increase in the number of studies on this topic, particularly for species management and conservation as well as the welfare of captive animals. The current knowledge of social organization in the European bison (*Bison bonasus*) is still largely based on descriptions of group compositions, most of which were obtained during opportunistic field observations. However, the numerous conservation programs for this species can only implement effective management decisions after the analysis of its social structures. For instance, the removal of a key individual can disturb the social stability of a group and thus indirectly affect the fitness of group members. This is the first study that uses social network analysis to examine the social structure of a semi-free ranging bison herd ($N = 14$). Closest neighbour associations are used to calculate the eigenvector centrality and individual social strength of each animal. These two indices are combined after a principal component analysis (PCA) to form the *Sociability* variable, which was then tested for correlations with age, dominance rank, number of matrilines and reproductive status (lactating *vs* non-lactating). Results reveal strong group cohesion, with a close association of individuals belonging to the same matriline within the herd. The cumulative distribution of the eigenvector centralities follows a linear function, meaning that no individual has a highly central position compared to its congeners. Finally, a high *Sociability* value was not correlated to age, dominance rank or number of matrilines, but was dependent on the reproductive status of females. These results indicate the necessity to consider the social welfare of animals, for instance by taking matrilineal relationships into account when making bison groups management decisions.

1. Introduction

Group living is an adaptive strategy that has multiple benefits for individuals (Alexander, 1974). Among the most obvious advantages, it decreases individual predation risk through the dilution effect and vigilance of congeners (Bertram, 1978; Delm, 1990), and

improves foraging through the sharing of information about resource location and quality (Couzin and Krause, 2003; Danchin et al., 2004; Valone, 1989). Group living also provides reproductive advantages by facilitating the meeting of breeding partners (Nordell and Valone, 1998) and ensuring better offspring survival through the protection (and for some species, the cooperative rearing) of young (Clutton-Brock et al., 2001; Gilchrist and Russell, 2007; Wright, 1998). Much less is known about how social life benefits the welfare and health of animals (Brent, 2015; Koene and Ipema, 2014; Sueur and Pelé, 2015). Indeed, some individuals act as a bridge or social glue for other group members and are thus central to group stability; their removal or their death can dismantle the existing social relationships and can trigger an increase in aggressive behaviours, causing injuries and deleterious effects related to stress (Coleing, 2009; Formica et al., 2012; Makagon et al., 2012). The viability of a population can therefore be strongly dependent on the social interactions between group members and this is of great importance for animal management, especially for wild endangered species (Archie and Chiyo, 2012; Kurvers et al., 2014; Snijders et al., 2017). One such species in Europe, the European bison (*Bison bonasus*), is particularly concerned by this problem.

The European bison is the largest herbivore on the European continent and is classified as vulnerable on the IUCN Red List (Krasińska and Krasiński, 2013; Olech, 2008). It is known to be a social species living in groups that vary in size and composition according to the

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season, *i.e.* a species with a fission-fusion dynamics (Krasińska et al., 2000; Krasiński, 1978). The basal unit is a mixed group composed of an average number of 20 individuals (Krasiński, 1967; Kulagin, 1919; Wróblewski, 1927). The group includes cows with their calves, sub-adults of both sexes aged two to three years old and occasionally adult bulls (> 4 years), especially during the mating season (Krasiński, 1967). Outside the rutting period, four- to six-year-old bulls tend to form bachelor groups of two to ten individuals while old males, often over the age of seven, remain solitary (Krasińska and Krasiński, 1995, 1994; Krasiński et al., 1994).

Long considered as game and affected by habitat fragmentation, expansion of agriculture and political conflicts, wild bison populations decreased and finally became extinct at the beginning of the 19th century (Krasińska and Krasiński, 2013; Pucek et al., 2004). In the 1920s, several countries decided to restore this emblematic species through a breeding program involving the few bison that had been kept in captivity and by the creation of the International Society for the Protection of the European Bison (Krasińska and Krasiński, 2013; Pucek et al., 2004; Sztolcman, 1924). These conservation efforts led to an increase in world population numbers, but the return to sufficient population levels is limited by habitat availability and economic constraints (Vlasakker, 2014). The insufficient overall scientific understanding of the ecology, behaviour and management of bison is also an obstacle to the establishment of new populations (Pucek, 1967; Pucek et al., 2004).

In particular, little is known about the social organisation of the species; the majority of the literature was written in the 19th and 20th centuries and mainly describes the demographic composition of groups. Contradictory results are also provided about the social links between group members, with some authors arguing that groups are composed of bison that are linked by kinship ties (Krasiński, 1978; Wróblewski, 1927), while others suggest that groups are not family units (Pucek et al., 2004). Understanding the nature and the strength of social links in European bison groups would allow us to identify the central individuals, *i.e.* those that are the most connected to others and are the most influential members of the group (Coleing, 2009; Makagon et al., 2012), thus enabling wildlife management teams to avoid selecting these individuals for transfers between populations in parks and natural reserves (Flack et al., 2006; Rose and Croft, 2015; Snijders et al., 2017). This information would improve the general welfare of group members by keeping their familial structure as intact as possible, and could eventually have a positive impact on reproductive success (Coleing, 2009; Koene and Ipema, 2014; Sueur and Pelé, 2015), which is a crucial issue for the European bison population of just over 4000 individuals (Krasińska and Krasiński, 2013).

In this context, we used social networks analysis based on spatial associations to investigate the social structure of a mixed European bison group (Croft et al., 2008; Krause et al., 2009; Wey et al., 2008). Spatial associations directly reflect social preferences between individuals in ungulates (Boissy and Dumont, 2002; Della-Rossa et al., 2013; McDonnell, 2003). Although our study concerns just one group, it is the first to assess the social network structure of European bison. This meant investigating whether the herd was organised around very central individuals, *i.e.* whether the social network was centralized or not (Sueur et al., 2012), and identifying the nature of the social links between group members. Mixed groups of European bison are commonly described to be headed by an adult female with a calf; this individual is usually the oldest and most dominant female (Krasiński, 1967, 1978). For many ungulate species, the oldest females have more experience and knowledge of their environment (Berry and Bercovitch, 2015; Ramos et al., 2015; Reinhardt, 1983), and their dominant positions in the hierarchy provide them with social power within the group (Caboń-Raczyńska et al., 1987; Rutberg, 1986). More generally, mature females in matriarchal societies often have strong established social relationships that favour the diffusion and the sharing of information as well as group cohesion (Archie and Chiyo, 2012; Carter et al., 2013a). Based on these general observations, we hypothesized that (1) the oldest dominant females would be key individuals in group social organisation and cohesion, *i.e.* they would be the most central members of the herd. However, juveniles maturing into young adults usually show immature behaviours and are more gregarious and less selective in their choices of associates (Carter et al., 2013a). This means that their centrality is often very high (Vander Wal et al., 2016) and could indirectly influence the centrality of their mothers. We therefore expected (2) to observe a higher social centrality for lactating females than for non-lactating ones.

In many ungulates, individuals maintain reciprocal and preferential relationships with other group members that are based on kin or affiliative interactions (Carter et al., 2013b; Dunbar and Shultz, 2010; Kimura, 1998). The latter are often at the core of subset structure in species that are characterized by a fission-fusion dynamics such as the European bison (Archie et al., 2006; Bercovitch and Berry, 2010; Lazo, 1994). We thus hypothesized that (3) bison would form a number of stable clusters composed of kin relatives and/or affiliates that could predetermine the composition of subgroups in the event of herd fission.

2. Methods

2.1. Ethics statement

This study was approved by our institutions (Institut Pluridisciplinaire Hubert Curien, ARK Nature, PWN) and was carried out in full accordance with ethical guidelines and European animal welfare legislation.

Animals were accustomed to the presence of observers and were observed at a reasonable and safe distance, without any handling or invasive intervention. Every effort was made to respect the welfare of the animals and minimize the disturbance of the herd.

2.2. Study area

Our study was conducted in the Kraansvlak area, which is part of the Zuid-Kennemerland National Park (3 800 ha) in the Netherlands (52°23′16.1″N, 4°34′41.3″E). This area measures 330 ha and is composed of six main habitats: sand dunes, grasslands, deciduous forest, pine forest, shrubland and scattered water ponds. Animal species found in the area include Konik horses (*Equus caballus gmelini Ant.*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), rabbits (*Oryctolagus cuniculus*), red foxes (*Vulpes vulpes*) and numerous bird, reptile and insect species. The natural predators of bison, namely grey wolves (*Canis lupus*) and brown bears (*Ursus arctos*), are not found in the Kraansvlak area.

2.3. Study subjects

The European bison herd studied here consisted of 14 individuals (Table 1), including eight adult females aged from four to fifteen years, two sub-adult females aged two and three years, two ten-month-old juvenile males and two juvenile females aged eight and nine months. This demographic composition corresponds to the typical demographic situation observed in natural conditions from April to June. The ages of these individuals and the kinship relationships between them were obtained from the pedigree book of the species, which contains the identity and the genetic information of all recorded captive and semi-captive animals. Unlike numerous European bison populations living in natural reserves, the Kraansvlak herd was not provided with food supplements during winter; this made them a reliable model for behavioural studies in natural conditions.

2.4. Data collection

Observers carried out preliminary observations over the three weeks preceding the data collection period to recognize each individual using

Table 1
Characteristics of each group member (Ind), taking into account the group social network (N = 14): age in months (Age), dominance rank (Dom), inversed dominance rank (Dom_inv), eigenvector centrality (Cent), individual social strength (Stren), *Experience* variable (scores obtained after the PCA 1 for Dim 1, represented by Age and Dom_inv) and *Sociability* variable (scores obtained after the PCA 1 for Dim 2, represented by Cent and Stren). The oldest and dominant individuals have positive and high *Experience* values; the individuals with high eigenvector centralities and social strengths have positive and high *Sociability* values.

Ind	Age	Dom	Dom_inv	Cent	Stren	*Experience*	*Sociability*
Kr	180	2	13	0.29	1120	2.147	1.554
Kg	132	5	10	0.27	1070	1.155	0.735
Kt	132	3	12	0.32	1119	1.265	1.671
Ko	102	1	14	0.32	1155	1.170	1.791
In	78	6	9	0.17	760	1.073	−2.323
Mo	78	8	7	0.19	858	0.520	−1.660
Wi	78	4	11	0.22	888	1.065	−0.993
Fr	54	7	8	0.21	897	0.262	−1.288
Ky	42	9	6	0.22	1000	−0.421	−0.776
Nr	30	10	5	0.29	855	−0.753	−0.726
Nl	10	12	3	0.32	1107	−1.825	0.741
Nm	10	11	4	0.20	1156	−1.343	−0.459
Nj	9	13	2	0.34	1194	−2.203	1.381
Nv	8	14	1	0.30	1095	−2.112	0.352

horn, tail, fur and hump characteristics. Throughout the data acquisition period (from 5th April 2016 to 22nd June 2016), the bison herd was observed between 09:30 and 16:30, for an average of 4 h per day. The daily observation time depended on the climatic conditions and the time required to locate the group. For the entire study period, the total observation time was 156 h. To avoid setting off stress behaviours and ensure that the presence of observers did not interfere with the natural behaviours and welfare of the herd, bison were observed at a distance of 20–50 m, depending on environmental conditions and habitat configuration (McHugh, 1958; Ramos et al., 2016, 2015).

2.4.1. *Affiliative relationships*

The observation of mutual grooming and social contacts behaviours is often used to investigate affiliative relationships in ungulates (Della-Rossa et al., 2013; Kimura, 1998; Mooring and Hart, 1993; Val-Laillet et al., 2009). It was difficult to use these data in our study, because these behaviours are rare in bison and only generally occur between a cow and her yearling calf (Krasińska and Krasiński, 2013). We therefore chose to identify affiliative bonds by examining social proximity, which also reflects affinities between the individuals (Briard et al., 2015; Kummer, 1970; McDonnell, 2003). Every 5 min, the identity of the nearest neighbour was recorded for each bison, *i.e.* the closest individual to the focus animal, using the *instantaneous sampling method* (Altmann, 1974). When there was an equal distance between the focus individual and several individuals, the identities of all the equidistant neighbours were recorded. This created a network called the “nearest-neighbour” network. The spatial proximities (based on the evaluation of inter-individual distances between every dyad, in meters) were also recorded every 5 min. This created a second network that was highly correlated to the first (Mantel Z-test; r = 0.743, p(perm) < 0.001). The network with lower observer bias, *i.e.* the “nearest-neighbour” network, was finally selected for the rest of our study (Farine and Whitehead, 2015; Franks et al., 2010)

The two observers did not move during the scans to avoid interference caused by movement. Data collection was suspended during any movement of the bison. Although some data was collected when certain group members were out of sight, only scans for which all the herd members were observed were considered for data analysis, *i.e.* a total of 511 scans.

2.4.2. *Dominance relationships*

The *continuous sampling method* (Altmann, 1974) was used to score all the uni-directional agonistic interactions, noting the identity of the emitter and that of the receiver for each interaction (Briard et al., 2015). Four types of behaviour were recorded: (1) threat of a horn hit, when an individual approaches another with its horns but does not finally have any physical contact, (2) aggression, when an individual hits another with a horn, (3) displacement, when an individual approaches another to a distance of up to one meter and the latter moves away, and (4) avoidance, when an individual comes within 5 m of another and the latter moves away.

2.5. *Data analyses*

The “nearest-neighbour” scans were used to create an asymmetrical matrix, hereafter referred to as a matrix of associations.

Table 2
Definitions of the individual and group social network indices used in the current study (Pasquaretta et al., 2014; Sueur et al., 2011).

Index	Technical definition	Meaning	Instances
Eigenvector centrality	The number and strength of associations of an individual, whilst taking into account the strength of associations of the individuals with whom it is itself associated.	How well an individual is connected to others, in terms of direct and indirect connections. Often described as “popularity”.	The centrality of an individual within the group increases with the eigenvector centrality value.
Social strength	The sum of the association indices of the focal individual with all other individuals.	How strongly an individual is directly connected to others. Often described as “social activity”.	A high strength value indicates that the individual has strong associations with other individuals, and/or many associations with other individuals.
Network density (*d*)	The sum of observed associations divided by the total number of possible associations.	The level of cohesiveness in the group.	A value of 0 indicates that no individuals are associated, whilst a value of 1 indicates that all individuals are associated to each other.
The centralisation index (*CI*)	The sum of the differences between each individual’s centrality and the centrality of the most central individual, divided by the sum of the differences of centralities calculated under the hypothesis of the social network characterized as a star network. The result obtained is then expressed in percentage.	How far a network is dominated by a single or a few individuals.	A value close to 0% indicates an equal or decentralized network, whilst a value close to 100% indicates a network that is centralized around one individual.
Modularity (Q)	The fraction of internal connections in each cluster, minus the expected fraction if connections had been distributed at random but with the same degree sequence.	How far a group is clustered.	A value close to 0 indicates a purely random distribution of relationships, whilst a value close to 1 indicates strong clustering with clearly identified subgroups/subsets.

2.5.1. Individual characteristics and social relationships

Based on the matrix of associations, we calculated different social network indices for each members of the herd (see Table 2 for detailed definitions of indices). The eigenvector centrality coefficient was used to determine the connectivity of an individual within its social network. This is calculated according to the number and strength of the relations between the individual and its congeners, while taking into account the association degree of the congeners to which it is connected (Wasserman and Faust, 1994). The individual with the highest eigenvector centrality index is therefore the most central individual in the herd. We also calculated individual social strength, *i.e.* the social activity of the individual, which corresponds to the sum of associations of the animal with all other group members (Whitehead, 2009). An individual with high social strength therefore has numerous and repetitive associations with other individuals.

We then positioned the given and received agonistic interactions for each pair of individuals on an asymmetrical matrix to investigate dominance relationships. SOCPROG 2.7 software (Whitehead, 2009) was used to analyse the matrix and measure the linearity of the hierarchy ($h' = 0.949$, $p < 0.0001$, 10 000 permutations; de Vries, 1995), which provided a dominance score for each animal, called the Modified David's Score (MDS). The 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, 2006). Dominant animals are therefore characterized by the highest positive MDS values, while subordinates show largely negative values (Gammell et al., 2003). Dominance ranks ranging from 1 to 14 were then calculated from these MDS (Table 1), where Rank 1 is assigned to the most dominant individual and Rank 14 corresponds to the least dominant (de Vries, 2006). The calculation of the rank difference for each pair of individuals provided a matrix of dominance rank differences.

For the needs of the study and because bison live in matriarchal societies (Krasińska and Krasiński, 2007), the number of matrilineal relatives was determined for each individual in the group. We also constructed matriline matrix codes of 1 and 0 for related and unrelated dyads, respectively. Finally, an age difference matrix was built for each pair of individuals.

2.5.2. Group network measures

We calculated three indices from the matrix of associations using SOCPROG 2.7 Software (Whitehead, 2009) to characterize the group social network (see Table 2 for detailed indices definitions). The first is network density (*d*), *i.e.* the number of observed associations divided by the total number of possible associations (Sueur et al., 2011). The centralization index (*CI*) evaluates the centrality level of the network, *i.e.* whether associations are organised around one or several very central individuals or not, using the following formula:

$$CI = \frac{\sum_i^N (Cmax - Ci)}{Max\sum_i^N (Cmax - Ci)} x\,100$$

where Ci represents the eigenvector centrality index of individual i, $Cmax$ is the highest eigenvector centrality index among group members and $Max\sum_i^N (Cmax - Ci)$ is the obtained value if the social network was characterized as a star network, *i.e.* organised around one highly central individual (Pasquaretta et al., 2014).

Modularity (Q) is the last of these three indexes. It indicates the division of the group into communities, considering that association indexes are generally high among individuals belonging to the same cluster and low among individuals of different clusters (Newman, 2006, 2004). A modularity value above 0.3 is considered to indicate a significant division of the group (Newman, 2004; Whitehead, 2009).

2.5.3. Statistical analyses

We determined the nature of the social network, *i.e.* random or scale-free (Bret et al., 2013), by ranking individuals from the highest to the lowest eigenvector centrality and then comparing the resulting distribution with linear and power distributions using linear regressions, previously validated by testing the normality of residuals with Shapiro-Wilk normality tests. In the case of a linear distribution, the network is qualified as a random social network (Erdös-Rényi type), *i.e.* the associations between individuals are set up in a random manner (Erdös and Rényi, 1960). However, the network is considered to be scale-free in the case of a power distribution, *i.e.* a large proportion of associations involve "hyper-central" individuals (Barabási and Albert, 1999).

SOCPROG 2.7 Software (Whitehead, 2009) was used to assess a cluster analysis of the matrix of associations. This analysis is based on the association index of individuals and determines a threshold beyond which they are considered to belong to the same cluster. The results are considered to be close to reality when the calculated cophenetic correlation coefficient (ranged from 0 to 1) approaches a value of 0.80 (Fry, 1993). We then assessed the reciprocity of associations with a Mantel Z-test (10 000 permutations). This test investigates the hypothesis that the interaction rate between individual A and individual B is correlated with that between B and A (Hemelrijk, 1990). Mantel Z-tests (10 000 permutations) were used to conduct matrix correlations, first between the matrix of associations and the matrices of age and dominance rank differences, and then between the matrices of associations and matrilines.

Age and dominance rank were highly correlated in the social network of the group (Pearson's correlation test: $r = -0.893$, $p(perm) = 0.001$). This was also true for eigenvector centrality and individual social strength (Pearson's correlation test: $r = 0.700$, $p(perm) = 0.006$). Given the high correlation of variables and the difficulty to ascertain whether age and eigenvector centrality were more influential than dominance and individual social strength for the social organisation of a group, a principal component analysis (PCA) was performed to group together and reduce the number of variables (Ledee et al., 2015; Viblanc et al., 2016). Rcmdr package and the plugin FactoMineR were used. The inversed dominance ranks were calculated, meaning that the individual with the highest rank (score = 1) had the inversed lowest score (score = 14). The PCA obtained has two main dimensions (Table 3); dimension 1 (Dim 1) explained 47.72% of the results and was composed of age (Age) and inversed dominance rank (Dom_inv), and dimension 2 (Dim 2) explained 42.27% of the results and was composed of eigenvector centrality (Cent) and individual social strength (Stren, Fig. 1A). Using the scores obtained for each dimension, two new variables were created, namely *Experience*, which groups together Age and Dom_inv, and *Sociability*, which groups together Cent and Stren (Table 1). The oldest and dominant individuals in the group social network had positive and high *Experience* values in Dim 1 while the individuals with high centralities and social strengths had positive and high *Sociability* values in Dim 2 (Fig. 1A).

Finally, Pearson's correlation tests were performed with

Table 3

Rotated component scores from the principal component analyses of the individual and social network indices for the whole group (PCA 1) and for the group after removing the juveniles (PCA 2).

	DIM 1	DIM 2	DIM 3
PCA 1			
Age	0.927	0.300	0.011
Dom_inv	0.955	0.193	0.004
Cent	−0.244	0.889	−0.386
Stren	−0.279	0.879	0.387
PCA 2			
Age	−0.906	0.394	−0.153
Dom_inv	−0.923	0.040	0.382
Cent	0.963	0.241	0.107
Stren	0.977	0.167	0.114

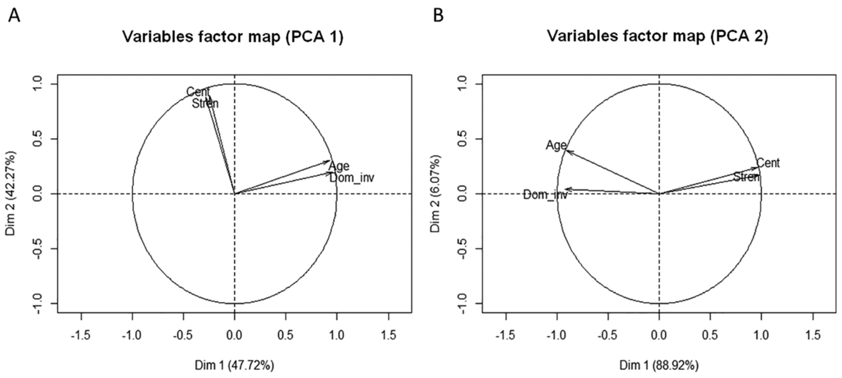

Fig. 1. Principal component analysis (PCA) of individual characteristics for group members A) with juveniles (PCA 1, N = 14) and B) without juveniles (PCA 2, N = 10). For A), dimension 1 (Dim 1) explains 47.72% of the results and is composed of age (Age) and inversed dominance rank (Dom_inv); dimension 2 (Dim 2) explains 42.27% of the results and is composed of eigenvector centrality (Cent) and individual social strength (Stren). The higher and more positive the value of Dim 1, the older and more dominant the individual will be. The higher and more positive the value of Dim 2, the more central the individual is and the higher its social strength will be. For B), dimension 1 (Dim 1) explains 88.92% of the results and is composed of Age, Dom_inv, Cent and Stren. Dimension 2 (Dim 2) explains 6.07% of the results. The higher and more positive the value of Dim 1 is, the older and more dominant the individual is and the less centrality and social strength it will have.

permutations (corPerm2 R function, 10 000 permutations) to study the influence of the *Experience* variable and the number of matrilineal relatives on the *Sociability* variable. A Student *t*-test was also conducted with permutations (t.perm R function, 10 000 permutations) to compare the *Sociability* values of lactating and non-lactating females.

Data for juveniles were then removed from the network analyses in order to exclude any potential influence of the mother-offspring relationship on the calculation of eigenvector centrality and social strength indexes of sub-adult and adult individuals. We then conducted a second PCA (Table 3) before performing a new Student *t*-test with permutations between lactating and non-lactating females. The second PCA has two main dimensions (Fig. 1B). Dimension 1 explained 88.92% of the results and was composed of Age, Dom_inv, Cent and Stren; dimension 2 explained 6.07% of the results.

Apart from the use of SOCPROG 2.7 Software (Whitehead, 2009) for social data analyses, all statistics were conducted in R Studio 1.0.44 Software (RStudio Team, 2016) with the significance level α set at 0.05. The social network of the group (Fig. 2) was based on the matrix of associations and was visualized using Gephi 0.9.1 Software (Bastian et al., 2009).

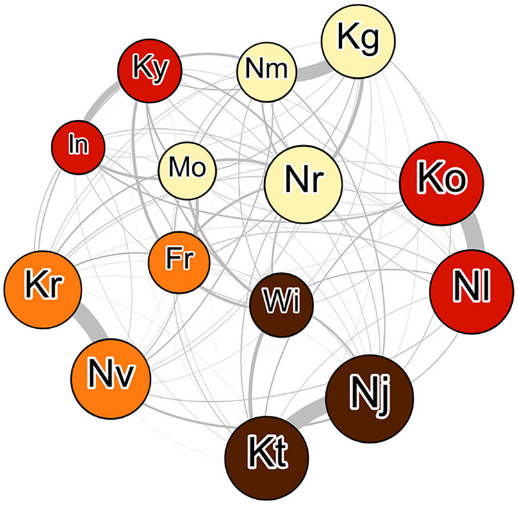

Fig. 2. Group social network representation. Matrilineal relatives have an identical node colour. Grey lines illustrate the associations between the individuals, and the thickness of the links is proportional to the frequency at which each individual was identified as the nearest neighbour of another ($Freq_{min}$ = 1, $Freq_{max}$ = 379). The size of the nodes is related to the eigenvector centrality index of individuals: the more central an individual is, the bigger the node will be. Individuals are located according to the spatial affinities they have with each other.

3. Results

3.1. Social network characteristics

All individuals in the group are connected with each other ($d = 1$) with an average occurrence of 36.413 between two individuals ($Freq_{min}$ = 1, $Freq_{max}$ = 379). There is no “hyper-central” individual and the group centrality index is very low (CI = 16.418%); the social network is thus categorized as a decentralized social network (Fig. 2). The distribution analysis of the centralities confirms the absence of a “hyper central” individual in the group: the distribution follows a more linear function than a power function, showing that the network is of a Erdös-Rényi type, *i.e.* random ($R^2_{lin} = 0.954 > R^2_{pow} = 0.686$, $y = -0.0135x + 0.3623$, $p < 0.001$).

The modularity is higher than the threshold value (Q = 0.366), indicating a significant probability that the group will be clustered. This is confirmed by the cluster analysis, which shows six different clusters with a cophenetic coefficient of 0.98 (Fig. 3). Two of these clusters are composed of cows and their yearling calves, two others include mothers, their yearling calves and their sub-adult/adult offspring, and the two remaining clusters are composed of close relatives and affiliated individuals.

3.2. Preferential associations between group members

The analysis of the matrix of associations shows a high reciprocity of associations (Mantel Z-test: r = 0.927, p(perm) < 0.001): preferential partner A of individual B also has individual B as its preferential

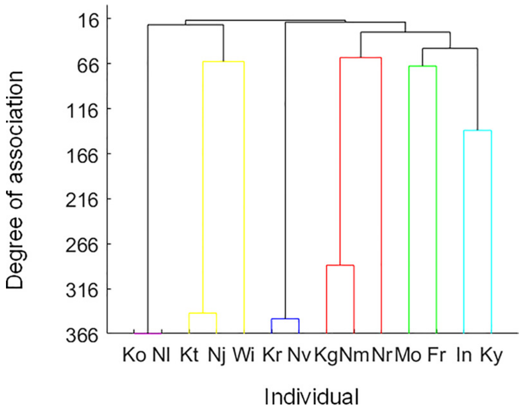

Fig. 3. Dendrogram representing the different clusters present within the group (N = 14) after a cluster analysis (cophenetic coefficient = 0.98, Q = 0.366). Clusters were obtained from the matrix of associations. Individuals belonging to the same cluster, *i.e.* individuals that have a high degree of association, have the same branch colour.

partner.

We observed a positive significant correlation between the matrix of associations and the age differences matrix (Mantel Z-test: $r = 0.197$, $p(\text{perm}) = 0.006$), indicating that individuals associate with individuals that differ from them not only in terms of age but also, indirectly, in terms of their dominance rank. This is confirmed by the positive significant correlation between the matrix of associations and the matrix of dominance rank differences (Mantel Z-test: $r = 0.208$, $p(\text{perm}) = 0.012$). These results may however be highly influenced by the mother-offspring links. Indeed, individuals preferentially associate with matrilineal relatives whatever their age or their dominance rank, as confirmed by the significant correlation between the matrices of associations and matrilines (Mantel Z-test: $r = 0.508$, $p(\text{perm}) < 0.001$). This last result is also confirmed by the graphical representation of the social network of the group, in which matrilineal relatives are revealed to be mostly spatially associated (Fig. 2). Only the individuals *Ky* and *In* do not strictly follow this pattern: they interacted frequently and were observed at a distance from their other relatives *Ko* and *Nl* (Fig. 2).

3.3. Individual characteristics and position in the social network

The *Sociability* variable is not significantly correlated with *Experience* (Pearson's correlation test: $r = -1.754 \times 10^{-4}$, $p(\text{perm}) = 1$). Nor can it be explained by the number of matrilineal relatives each individual has in the group (Pearson's correlation test: $r = -0.297$, $p(\text{perm}) = 0.291$). However, the *Sociability* value is significantly higher for lactating females than for females without a calf (Student *t*-test: $t = -7.897$, $p(\text{perm}) = 0.005$; Fig. 4A). The opposite result was found when juveniles were removed from the analyses (Fig. 4B): in this case, lactating females had the weakest centralities and the weakest individual social strength of associations (Student *t*-test: $t = -7.896$, $p(\text{perm}) = 0.004$).

4. Discussion

To our knowledge, this is the first study reporting the social network data of a herd of European bison. We first studied the general properties of the group social network and showed that all individuals were connected to each other, with a density value of 1. This indicates that the group was very cohesive. There is, however, a large disparity between the occurrences of associations for the different individuals, with some pairs observed together more frequently than others. Thus, although social cohesion was high, there were preferential associations between the herd members. This is confirmed by the modularity measure, which was above the threshold value and indicated a high probability that the group would split into subgroups. Six clusters were identified in the network with a high cophenetic coefficient; these were mostly composed of mother-calf pairs, with some including the older offspring sub-adult or adult, whilst others contained more distant relatives or affiliated individuals. Kin associations were supported by a positive correlation between the matrices of associations and matrilines: the individuals of a same given matriline were highly spatially associated. This pattern of associations is found in many species (Clutton-Brock, 2002) and has been well described in several ungulate species (Carpenter, 2010). In the African elephant *(Loxodonta africana)*, maternal relatives most often stay together in the same group and associate within subgroups when the core group splits (Archie et al., 2006; Archie and Chiyo, 2012). In feral cattle (*Bos taurus*), Lazo (1994, 1992) observed two levels of social organisation: a low level at which animals formed unstable groups that changed in size and composition according to the fission or the fusion of subgroups, and a high level of social organisation within these subgroups. The advantages of these two levels of social organisation can be numerous, especially in an environment that has heterogeneous abundance and distribution of food or fluctuations in predator risks (Lazo, 1994; Prins, 1989). For instance, large groups can split when competition increases while allowing individuals to keep cooperative relationships by remaining in subgroups of kin relatives (Archie et al., 2006; Cameron et al., 2009; Emlen, 1995). More generally and as reported by the literature, a high degree of relatedness between interacting individuals may enhance their fitness by playing a role in the rearing and survival of offspring, for instance through the cooperative defence of calves (Hamilton, 1964; Pope, 2000; Pusenius et al., 1998). In support of our third stated hypothesis and in line with the literature on other ungulate species, the bison herd studied in this study remained very cohesive while being mostly composed of several stable clusters of matrilineal relatives that can predetermine the composition of the subgroups in the event of herd fission. The only individuals that did not follow this pattern were two females, *Ky* and *In*, which formed a pair apart from the others and had little contact with their other matrilineal relatives, *Ko* and *Nl.* Their low centrality or dominance rank could have made them both move away from *Ko*, the most dominant female in the group. Indeed, a number of studies have shown that subordinates tend to avoid dominant individuals as preferred partners, probably to prevent the numerous aggressions occurring between individuals of very different ranks (Briard et al., 2015; Syme et al., 1975). The second hypothesis to explain our observation would be *Ko*'s more highly developed maternal behaviour towards her yearling calf *Nl,* which made her less tolerant of her other relatives.

The other pattern of associations frequently observed in ungulates is assortativity according to age or dominance rank (Appleby, 1983; Bercovitch and Berry, 2013; Kimura, 1998). Group members of similar age or hierarchical status tend to be affiliated according to their similarities in social behaviour, physical condition or developmental requirements (Guilhem et al., 2000; Murray, 1981; Ruckstuhl, 2007; Villaret and Bon, 1998). For instance, the associations observed in calves in several species probably reflect a preference for playing partners with similar physical strength and skills, which especially serves as training for future adult interactions (Fagen, 1981; Rothstein and Griswold, 1991; Thompson, 1996). However, no association

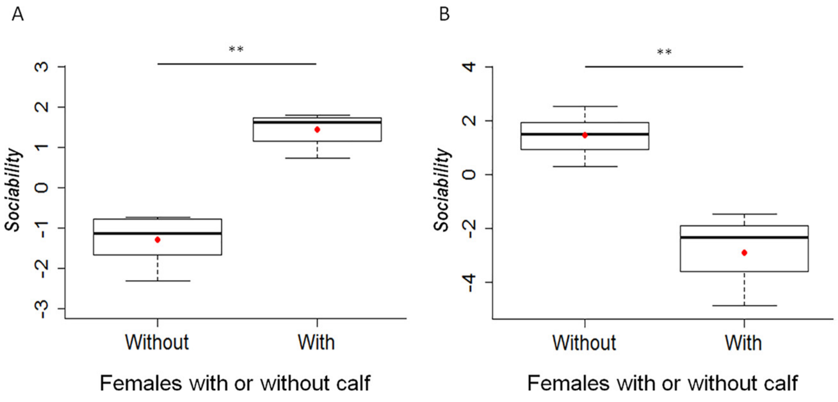

Fig. 4. Boxplot representing the values of the *Sociability* variable for females without calves (Without, N = 6) and females with a calf (With, N = 4). Calves are taken into account in social network analyses for A) but not for B). The horizontal black lines represent the median and red dots indicate the mean of each category. (**: $p < 0.01$).

preference for similar age or dominance rank individuals was observed in our bison herd. These results could be explained by the importance of matrilineal subgroups in the social structure basis. These subgroups strongly associate close relatives whatever their age or their rank, at the expense of associations through similarities (Godde et al., 2015). Maternal bonds would be thus the main condition for social preference formation in European bison, as described in other matriarchal ungulate societies (Bashaw et al., 2007; Reinhardt and Reinhardt, 1981; Tulloch, 1978). These bonds can also explain the high reciprocity of associations we observed in the herd, especially through the dyadic and co-dependent nature of maternal behaviours and the high level of cooperation between closely related individuals (Cassinello and Calabuig, 2008; Makagon et al., 2012; Nituch et al., 2008). Finally, our findings suggest that bison are capable of fine-scale kin recognition, as reported in other ungulates (Cassinello and Calabuig, 2008; Ceacero et al., 2007; Ligout et al., 2004).

For individual network properties, the distribution of eigenvector centralities followed a linear distribution and the group centrality index was very low, indicating that, in contrast to our first hypothesis, there is no highly central individual in the group (Kanngiesser et al., 2011). The small size of the herd could explain this network property, as suggested by James et al. (2009) who stated that scale-free networks were difficult to observe in small social groups. However, a study by Kanngiesser et al. (2011) showed that both scale-free and random networks can be theoretically obtained for small sample size (N = 17). An alternative hypothesis to explain the random property of our network could therefore be that the herd do not need the presence of a highly central individual to maintain social cohesion or to take group decisions (Foley et al., 2008; Lusseau and Newman, 2004; Modlmeier et al., 2014). Natural herd cohesion could exist despite the presence of distinct subgroups because all herd members are interconnected by primary, or at least secondary, kin bonds (Taylor and Sussman, 1985; Wiszniewski et al., 2010). The absence of predators in the Kraansvlak area as well as the wide availability and distribution of food resources across the zone, especially in grassland areas, could also make it less important to have a key individual for group survival (Aplin et al., 2012; Foster et al., 2012; McComb et al., 2011). More systematic analyses of European bison groups with different compositions are needed to confirm this hypothesis.

Contrary to our expectations, *Sociability* was not correlated with age and dominance rank (the *Experience* variable in our study). These results are not consistent with the literature for ungulates. For instance, older African elephant individuals are socially connected to many other individuals and are thus very central within their group (McComb et al., 2001). Conversely, juvenile roan antelopes (*Hippotragus equinus*) associate strongly with each other and have higher centrality in the herd than the adults (Carpenter, 2010). Studies describing other ungulate species have suggested that subordinate cows groom dominant congeners more than *vice versa*, which implies that the centrality of dominants is higher than that of subordinates because of their high attractiveness (Carpenter, 2010; Reinhardt et al., 1986). The results of the present study could be explained by the presence of juveniles in the group composition, which may strongly affect the link between centrality, dominance rank and age. This occurs either actively, through a stronger association between juveniles and their mother, or passively, when juveniles change the associations between their mother and her partners through their own associations, particularly during the weaning period. At this period, calves are more independent and spend more time interacting and playing with other calves (Rothstein and Griswold, 1991; Thompson, 1996; Vitale et al., 1986) before increasing their interactions with other members of the group (Carter et al., 2013a; Keeling, 2001). Even so, and despite this growing socialisation, calves remain very close to their mother to ensure their nutritional needs until they are totally independent: they thus indirectly influence the association patterns of their mothers (Bertrand et al., 1996; Estep et al., 1993; Lawrence and Wood-Gush, 1988; Poindron et al., 1994). This assumption is supported by the values of the *Sociability* variable, which were significantly higher for lactating females than for females without calves, in line with our second hypothesis. After the removal of the calves from our analyses and the renewed performance of PCA, the older and more dominant females, which were also those with dependent calves, were the least central individuals. Ultimately, given that the centrality of individuals was calculated according to spatial associations (*i.e.* the “nearest-neighbour” network), this result means that the oldest dominant females tend to stay on the periphery of the group. This behaviour could be a strategy to protect their calves, because the danger is higher at the periphery than in the center of the group (Burger and Gochfeld, 1994; Hamilton, 1971; Hunter and Skinner, 1998).

The global results of this first study of the social network structure in European bison provide fundamental knowledge about the social organization of a herd and provide a first solution to the lack of data and the approximations found in the literature to date. However, the limitations of this study in terms of sample size and study duration mean that further studies are necessary before these conclusions can be generalized to the whole species.

5. Conclusion

The bison herd studied here showed a very high level of cohesion that was probably due to the predominance of kin relationships. The mostly matrilineal association pattern described here is commonly observed in several ungulate species (Archie et al., 2006; Carpenter, 2010; Lazo, 1994, 1992) and can predict the composition of subgroups formed during fission events. Association with very close relatives can confer numerous advantages through cooperative behaviours and can positively influence reproductive success (Archie and Chiyo, 2012; Pope, 2000; Pusenius et al., 1998). Even if the choice of partners by individuals is limited in semi-free roaming conditions, animals may experience less stress with kin individuals than with non-relatives. It would therefore be valuable to take these results into account for the conservation of European bison by keeping maternal association patterns as intact as possible in the event of individual transfers. The main aims of these transfers, namely to achieve genetic mixing and avoid consanguinity (Snijders et al., 2017; Sueur and Pelé, 2015), largely ignore the importance of social welfare in the context of conservation. For now, further studies on different herd sizes and compositions are needed to conclude upon a general pattern of social organisation in this species and consider how future conservation efforts should be shaped. This case study is the first to provide information that could play a role in developing innovative herd management strategies that take the social environment of animals into account while considering the intrinsic constraints of species conservation.

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References

Alexander, R.D., 1974. The evolution of social behavior. Annu. Rev. Ecol. Syst. 5, 325–383.

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227–266. https://doi.org/10.1163/156853974X00534.

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Sheldon, B.C., 2012. Social networks predict patch discovery in a wild population of songbirds. Proc. R. Soc. Lond., B, Biol. Sci. https://doi.org/10.1098/rspb.2012.1591. rspb20121591.

Appleby, M.C., 1983. Competition in a red deer stag social group: rank, age and relatedness of opponents. Anim. Behav. 31, 913–918. https://doi.org/10.1016/S0003-3472(83)80246-2.

Archie, E.A., Chiyo, P.I., 2012. Elephant behaviour and conservation: social relationships, the effects of poaching, and genetic tools for management. Mol. Ecol. 21, 765–778.

Archie, E.A., Moss, C.J., Alberts, S.C., 2006. The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. Proc. R. Soc. Lond., B, Biol. Sci. 273, 513–522. https://doi.org/10.1098/rspb.2005.3361.

Barabási, A.-L., Albert, R., 1999. Emergence of scaling in random networks. science 286, 509–512.

Bashaw, M.J., Bloomsmith, M.A., Maple, T.L., Bercovitch, F.B., 2007. The structure of social relationships among captive female giraffe (*Giraffa camelopardalis*). J. Comp. Psychol. 121, 46.

Bastian, M., Heymann, S., Jacomy, M., 2009. Gephi: an open source software for exploring and manipulating networks. ICWSM 8, 361–362.

Bercovitch, F.B., Berry, P.S.M., 2013. Age proximity influences herd composition in wild giraffe. J. Zool. 290, 281–286. https://doi.org/10.1111/jzo.12039.

Bercovitch, F.B., Berry, P.S.M., 2010. Ecological determinants of herd size in the Thornicroft's giraffe of Zambia. Afr. J. Ecol. 48, 962–971. https://doi.org/10.1111/j.1365-2028.2009.01198.x.

Berry, P.S.M., Bercovitch, F.B., 2015. Leadership of herd progressions in the Thornicroft's giraffe of Zambia. Afr. J. Ecol. 53, 175–182. https://doi.org/10.1111/aje.12173.

Bertram, B.C., 1978. Living in groups: predators and prey. Behav. Ecol. 64–96.

Bertrand, M.R., DeNicola, A.J., Beissinger, S.R., Swihart, R.K., 1996. Effects of parturition on home ranges and social affiliations of female white-tailed deer. J. Wildl. Manag. 899–909.

Boissy, A., Dumont, B., 2002. Interactions between social and feeding motivations on the grazing behaviour of herbivores: sheep more easily split into subgroups with familiar peers. Appl. Anim. Behav. Sci. 79, 233–245. https://doi.org/10.1016/S0168-1591(02)00152-1.

Brent, L.J., 2015. Friends of friends: are indirect connections in social networks important to animal behaviour? Anim. Behav. 103, 211–222.

Bret, C., Sueur, C., Ngoubangoye, B., Verrier, D., Deneubourg, J.-L., Petit, O., 2013. Social structure of a semi-free ranging group of mandrills (*Mandrillus sphinx*): a social network analysis. PLoS One 8, e83015.

Briard, L., Dorn, C., Petit, O., 2015. Personality and affinities play a key role in the organisation of collective movements in a group of domestic horses. Ethology 121, 888–902. https://doi.org/10.1111/eth.12402.

Burger, J., Gochfeld, M., 1994. Vigilance in African mammals: differences among mothers, other females, and males. Behaviour 131, 153–169.

Caboń-Raczyńska, K., Krasińska, M., Krasiński, Z.A., Wójcik, J.M., 1987. Bisoniana XCVII. Rhythm of daily activity and behavior of European bison in the Białowieża Forest in the period without snow cover. Acta Theriol. (Warsz.) 32, 335–372.

Cameron, E.Z., Setsaas, T.H., Linklater, W.L., 2009. Social bonds between unrelated females increase reproductive success in feral horses. Proc. Natl. Acad. Sci. 106, 13850–13853.

Carpenter, L.D., 2010. Utilizing Social Networks Analysis in the Characterization of African Ungulate Social Structure (Master Degree Report). Maryland, College Park. .

Carter, K.D., Brand, R., Carter, J.K., Shorrocks, B., Goldizen, A.W., 2013a. Social networks, long-term associations and age-related sociability of wild giraffes. Anim. Behav. 86, 901–910.

Carter, K.D., Seddon, J.M., Frère, C.H., Carter, J.K., Goldizen, A.W., 2013b. Fission–fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. Anim. Behav. 85, 385–394.

Cassinello, J., Calabuig, G., 2008. Spatial association in a highly inbred ungulate population: evidence of fine-scale kin recognition. Ethology 114, 124–132.

Ceacero, F., Landete-Castillejos, T., García, A.J., Estévez, J.A., Gallego, L., 2007. Kinship discrimination and effects on social rank and aggressiveness levels in Iberian red deer hinds. Ethology 113, 1133–1140.

Clutton-Brock, T., 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. Science 296, 69–72.

Clutton-Brock, T.H., Russell, A.F., Sharpe, L.L., Brotherton, P.N.M., McIlrath, G.M., White, S., Cameron, E.Z., 2001. Effects of helpers on juvenile development and survival in meerkats. Science 293, 2446–2449.

Coleing, A., 2009. Research article The application of social network theory to animal behaviour. Biosci. Horiz. 2, 32–43.

Couzin, I.D., Krause, J., 2003. Self-organization and Collective Behavior in Vertebrates, in: Behavior, B.-A. In the S. Of (Ed.). Academic Press, pp. 1–75.

Croft, D.P., James, R., Krause, J., 2008. Exploring Animal Social Networks. Princeton University Press.

Danchin, É., Giraldeau, L.-A., Valone, T.J., Wagner, R.H., 2004. Public information: from nosy neighbors to cultural evolution. Science 305, 487–491. https://doi.org/10.1126/science.1098254.

de Vries, 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.

de Vries, H., 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim. Behav. 50, 1375–1389. https://doi.org/10.1016/0003-3472(95)80053-0.

Della-Rossa, L., Chadœuf, J., Boissy, A., Dumont, B., 2013. Leaders of spontaneous group movements influence whole-group social organization: an experimental study on grazing heifers. Behaviour 150, 153–173. https://doi.org/10.1163/1568539X-00003043.

Delm, M.M., 1990. Vigilance for predators: detection and dilution effects. Behav. Ecol. Sociobiol. 26, 337–342. https://doi.org/10.1007/BF00171099.

Dunbar, R.I., Shultz, S., 2010. Bondedness and sociality. Behaviour 147, 775–803.

Emlen, S.T., 1995. An evolutionary theory of the family. Proc. Natl. Acad. Sci. 92, 8092–8099.

Erdös, P., Rényi, A., 1960. On the evolution of random graphs. Publ Math Inst Hung Acad Sci 5, 43.

Estep, D.Q., Crowell-Davis, S.L., Earl-Costello, S.-A., Beatey, S.A., 1993. Changes in the social behaviour of drafthorse (*Equus caballus*) mares coincident with foaling. Appl. Anim. Behav. Sci. 35, 199–213. https://doi.org/10.1016/0168-1591(93)90137-E.

Fagen, R., 1981. Animal play behavior.

Farine, D.R., Whitehead, H., 2015. Constructing, conducting and interpreting animal social network analysis. J. Anim. Ecol. 84, 1144–1163. https://doi.org/10.1111/1365-2656.12418.

Flack, J.C., Girvan, M., de Waal, F.B.M., Krakauer, D.C., 2006. Policing stabilizes construction of social niches in primates. Nature 439, 426–429. https://doi.org/10.1038/nature04326.

Foley, C., Pettorelli, N., Foley, L., 2008. Severe drought and calf survival in elephants. Biol. Lett. 4, 541–544.

Formica, V.A., Wood, C.W., Larsen, W.B., Butterfield, R.E., Augat, M.E., Hougen, H.Y., Brodie, E.D., 2012. Fitness consequences of social network position in a wild population of forked fungus beetles (*Bolitotherus cornutus*). J. Evol. Biol. 25, 130–137. https://doi.org/10.1111/j.1420-9101.2011.02411.x.

Foster, E.A., Franks, D.W., Morrell, L.J., Balcomb, K.C., Parsons, K.M., van Ginneken, A., Croft, D.P., 2012. Social network correlates of food availability in an endangered population of killer whales, Orcinus orca. Anim. Behav. 83, 731–736.

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.

Fry, J.C., 1993. Biological Data Analysis: a Practical Approach. Oxford University Press, Inc., New York, NY, USA.

Gammell, M.P., Vries, Hde, 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. Anim. Behav. 66, 601–605.

Gilchrist, J.S., Russell, A.F., 2007. Who cares? Individual contributions to pup care by breeders vs non-breeders in the cooperatively breeding banded mongoose (*Mungos mungo*). Behav. Ecol. Sociobiol. 61, 1053–1060.

Godde, S., Côté, S.D., Réale, D., 2015. Female mountain goats, *Oreamnos americanus*, associate according to kinship and reproductive status. Anim. Behav. 108, 101–107.

Guilhem, C., Bideau, E., Gerard, J.F., Maublanc, M.L., 2000. Agonistic and proximity patterns in enclosed mouflon (*Ovis gmelini*) ewes in relation to age, reproductive status and kinship. Behav. Processes 50, 101–112.

Hamilton, W.D., 1971. Geometry for the selfish herd. J. Theor. Biol. 31, 295–311.

Hamilton, W.D., 1964. The genetical evolution of social behaviour. II. J. Theor. Biol. 7, 17–52.

Hemelrijk, C.K., 1990. A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. J. Theor. Biol. 143, 405–420.

Hunter, L.T.B., Skinner, J.D., 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour 135, 195–211. https://doi.org/10.1163/156853998793066320.

James, R., Croft, D.P., Krause, J., 2009. Potential banana skins in animal social network analysis. Behav. Ecol. Sociobiol. 63, 989–997.

Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J., Call, J., 2011. Grooming network cohesion and the role of individuals in a captive chimpanzee group. Am. J. Primatol. 73, 758–767.

Keeling, J.L., 2001. Social Behavior in Farm Animals. CABI.

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.

Krasińska, M., Krasiński, Z.A., 2013. European Bison: The Nature Monograph. Springer Science & Business Media.

Krasińska, M., Krasiński, Z.A., 2007. European bison. Nat. Monogr. Mammal Res. Inst. PAS Bialowieża 318.

Krasińska, M., Krasiński, Z.A., 1995. Composition, group size, and spatial distribution of European bison bulls in Białowieża Forest. Acta Theriol. (Warsz.) 40, 1–21.

Krasińska, M., Krasiński, Z.A., 1994. Spatial structure of the European bison population in the Polish part of the Białowieża Forest 1976–1993. Parki Nar. Rezerwaty Przyr. 13, 69–87.

Krasińska, M., Krasiński, Z.A., Bunevich, A.N., 2000. Bisoniana 121. Factors affecting the variability in home range size and distribution in European bison in the Polish and Belarussian parts of the Białowieża Forest. Acta Theriol. (Warsz.) 45, 321–334.

Krasiński, Z., 1967. Bisoniana XXIV. Free living European bison. Acta Theriol. (Warsz.) 12, 391–405.

Krasiński, Z.A., 1978. Bisoniana LXVII. Dynamics and structure of the European bison population in the Białowieża Primeval Forest. Acta Theriol. (Warsz.) 23, 3–48.

Krasiński, Z.A., Bunevich, A.N., Krasińska, M., 1994. Characteristics of the European bison populations in the Polish and Belarussian parts of the Białowieża Forest. Parki Nar. Rezerwaty Przyr. 13, 25–67.

Krause, J., Lusseau, D., James, R., 2009. Animal social networks: an introduction. Behav. Ecol. Sociobiol. 63, 967–973. https://doi.org/10.1007/s00265-009-0747-0.

Kulagin, N.M., 1919. Zubry Beloveźskoj Pušči.

Kummer, H., 1970. Spacing mechanisms in social behavior. Inf. Int. Soc. Sci. Counc. 9, 109–122. https://doi.org/10.1177/053901847000900606.

Kurvers, R.H.J.M., Krause, J., Croft, D.P., Wilson, A.D., Wolf, M., 2014. The evolutionary and ecological consequences of animal social networks: emerging issues. Trends Ecol. Evol. (Amst.) 29, 326–335.

Lawrence, A.B., Wood-Gush, D.G.M., 1988. Home-range behaviour and social organization of Scottish blackface sheep. J. Appl. Ecol. 25, 25–40. https://doi.org/10.2307/2403607.

Lazo, A., 1994. Social segregation and the maintenance of social stability in a feral cattle population. Anim. Behav. 48, 1133–1141. https://doi.org/10.1006/anbe.1994.1346.

Lazo, A., 1992. Facteurs déterminants du comportement grégaire de bovins retournés à l'état sauvage. Rev. Ecol. 47, 51–66.

Ledee, E.J., Heupel, M.R., Tobin, A.J., Knip, D.M., Simpfendorfer, C.A., 2015. A comparison between traditional kernel-based methods and network analysis: an example from two nearshore shark species. Anim. Behav. 103, 17–28.

Ligout, S., Sebe, F., Porter, R.H., 2004. Vocal discrimination of kin and non-kin agemates among lambs. Behaviour 141, 355–369. https://doi.org/10.1163/156853904322981905.

Lusseau, D., Newman, M.E.J., 2004. Identifying the role that animals play in their social networks. Proc. R. Soc. Lond., B, Biol. Sci. 271, S477–S481. https://doi.org/10.1098/rsbl.2004.0225.

Makagon, M.M., McCowan, B., Mench, J.A., 2012. How can social network analysis contribute to social behavior research in applied ethology? Appl. Anim. Behav. Sci., Special Issue: Living In Large Groups 138, 152–161. https://doi.org/10.1016/j.applanim.2012.02.003.

McComb, K., Moss, C., Durant, S.M., Baker, L., Sayialel, S., 2001. Matriarchs as repositories of social knowledge in African elephants. Science 292, 491–494. https://doi.org/10.1126/science.1057895.

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. Lond., B, Biol. Sci. https://doi.org/10.1098/rspb.2011.0168. rspb20110168.

McDonnell, S., 2003. Practical Field Guide to Horse Behavior: the Equid Ethogram. Lexington. .

McHugh, T., 1958. Social behavior of the American buffalo (*Bison bison bison*). Zoologica 43, 1–40.

Modlmeier, A.P., Keiser, C.N., Watters, J.V., Sih, A., Pruitt, J.N., 2014. The keystone individual concept: an ecological and evolutionary overview. Anim. Behav. 89, 53–62.

Mooring, M.S., Hart, B.L., 1993. Effects of relatedness, dominance, age, and association on reciprocal allogrooming by captive impala. Ethology 94, 207–220. https://doi.org/10.1111/j.1439-0310.1993.tb00561.x.

Murray, M.G., 1981. Structure of association in impala, Aepyceros melampus. Behav. Ecol. Sociobiol. 9, 23–33. https://doi.org/10.1007/BF00299849.

Newman, M.E.J., 2006. Modularity and community structure in networks. Proc. Natl. Acad. Sci. 103, 8577–8582. https://doi.org/10.1073/pnas.0601602103.

Newman, M.E.J., 2004. Analysis of weighted networks. Phys. Rev. E 70, 056131.

Nituch, L.A., Schaefer, J.A., Maxwell, C.D., 2008. Fine-scale spatial organization reflects genetic structure in sheep. Ethology 114, 711–717.

Nordell, S.E., Valone, T.J., 1998. Mate choice copying as public information. Ecol. Lett. 1, 74–76.

Olech, W., 2008. *Bison bonasus*. IUCN Red List Threat. Species. URL http://www.iucnredlist.org/details/2814/0 (accessed 1.3.17).

Pasquaretta, C., Levé, M., Claidiere, N., Van de Waal, E., Whiten, A., MacIntosh, A.J., Pelé, M., Bergstrom, M.L., Borgeaud, C., Brosnan, S.F., 2014. Social networks in primates: smart and tolerant species have more efficient networks. others. Sci. Rep. 4, 7600.

Poindron, P., Caba, M., Arrati, P.G., Krehbiel, D., Beyer, C., 1994. Responses of maternal and non-maternal ewes to social and mother-young separation. Behav. Processes 31, 97–110.

Pope, T.R., 2000. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). Behav. Ecol. Sociobiol. 48, 253–267.

Prins, H.H.T., 1989. Buffalo herd structure and its repercussions for condition of individual African buffalo cows. Ethology 81, 47–71.

Pucek, Z., 1967. Bisoniana XXXV. The most important problems for further studies on European bison. Acta Theriol. (Warsz.) 12, 495–501.

Pucek, Z., Belousova, I., Krasinska, M., Krasinski, Z., Olech, W., 2004. Status Survey and Conservation Action Plan: European Bison. IUCNSSC Bison Spec. Group–Gland IUCN.

Pusenius, J., Viitala, J., Marienberg, T., Ritvanen, S., 1998. Matrilineal kin clusters and their effect on reproductive success in the field vole Microtus agrestis. Behav. Ecol. 9, 85–92.

Ramos, A., Petit, O., Longour, P., Pasquaretta, C., Sueur, C., 2016. Space Use and movement patterns in a semi-free-ranging herd of European bison (*Bison bonasus*). PLoS One 11, e0147404. https://doi.org/10.1371/journal.pone.0147404.

Ramos, A., Petit, O., Longour, P., Pasquaretta, C., Sueur, C., 2015. Collective decision making during group movements in European bison, Bison bonasus. Anim. Behav. 109, 149–160. https://doi.org/10.1016/j.anbehav.2015.08.016.

Reinhardt, C., Reinhardt, A., Reinhardt, V., 1986. Social behaviour and reproductive performance in semi-wild Scottish Highland cattle. Appl. Anim. Behav. Sci. 15, 125–136. https://doi.org/10.1016/0168-1591(86)90058-4.

Reinhardt, V., 1983. Movement orders and leadership in a semi-wild cattle herd. Behaviour 83, 251–264. https://doi.org/10.1163/156853983X00183.

Reinhardt, V., Reinhardt, A., 1981. Cohesive relationships in a cattle herd (*Bos Indicus*). Behaviour 77, 121–150. https://doi.org/10.1163/156853981X00194.

Rose, P.E., Croft, D.P., 2015. The potential of Social Network Analysis as a tool for the management of zoo animals. Anim. Welf. 24, 123–138.

Rothstein, A., Griswold, J.G., 1991. Age and sex preferences for social partners by juvenile bison bulls, Bison bison. Anim. Behav. 41, 227–237. https://doi.org/10.1016/S0003-3472(05)80474-9.

Team, R.Studio, 2016. RStudio: Integrated Development Environment for R, RStudio: Integrated Development for R. RStudio. RStudio, Inc., Boston, MA.

Ruckstuhl, K.E., 2007. Sexual segregation in vertebrates: proximate and ultimate causes. Integr. Comp. Biol. 47, 245–257. https://doi.org/10.1093/icb/icm030.

Rutberg, A.T., 1986. Dominance and its fitness consequences in American bison cows. Behaviour 96, 62–91. https://doi.org/10.1163/156853986X00225.

Snijders, L., Blumstein, D.T., Stanley, C.R., Franks, D.W., 2017. Animal social network theory can help wildlife conservation. Trends Ecol. Evol. (Amst.) 32, 567–577.

Sueur, C., Deneubourg, J.-L., Petit, O., 2012. From social network (centralized vs. decentralized) to collective decision-making (unshared vs. Shared consensus). PLoS One 7, e32566. https://doi.org/10.1371/journal.pone.0032566.

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'éthologie Et à l'écologie, Modélisations, Simulations, Systèmes Complexes. pp. 445–468.

Sueur, C., Petit, O., De Marco, A., Jacobs, A.T., Watanabe, K., Thierry, B., 2011. A comparative network analysis of social style in macaques. Anim. Behav. 82, 845–852. https://doi.org/10.1016/j.anbehav.2011.07.020.

Syme, L.A., Syme, G.J., Waite, T.G., Pearson, A.J., 1975. Spatial distribution and social status in a small herd of dairy cows. Anim. Behav. 23, 609–614.

Sztolcman, J., 1924. Matériaux pour l'histoire naturelle et pour l'historique du bison d'Europe (*Bison bonasus* Linn.). Annales Zoologici Musei Polonici Historiae Naturalis. pp. 49–136.

Taylor, L., Sussman, R.W., 1985. A preliminary study of kinship and social organization in a semi-free-ranging group of Lemur catta. Int. J. Primatol. 6, 601–614. https://doi.org/10.1007/BF02692291.

Thompson, K.V., 1996. Play-partner preferences and the function of social play in infant sable antelope, Hippotragus niger. Anim. Behav. 52, 1143–1155. https://doi.org/10.1006/anbe.1996.0261.

Tulloch, D.G., 1978. The water buffalo, *Bubalus bubalis*, in Australia: grouping and home range. Aust. Wildl. Res. 5, 327–354.

Val-Laillet, D., Guesdon, V., Von Keyserlingk, M.A., De Passillé, A.M., Rushen, J., 2009. Allogrooming in cattle: relationships between social preferences, feeding displacements and social dominance. Appl. Anim. Behav. Sci. 116, 141–149.

Valone, T.J., 1989. Group foraging, public information, and patch estimation. Oikos 357–363.

Vander Wal, E., Gagné-Delorme, A., Festa-Bianchet, M., Pelletier, F., 2016. Dyadic associations and individual sociality in bighorn ewes. Behav. Ecol. 27, 560–566. https://doi.org/10.1093/beheco/arv193.

Viblanc, V.A., Pasquaretta, C., Sueur, C., Boonstra, R., Dobson, F.S., 2016. Aggression in Columbian ground squirrels: relationships with age, kinship, energy allocation, and fitness. Behav. Ecol arw098.

Villaret, J.-C., Bon, R., 1998. Sociality and relationships in Alpine ibex (*Capra ibex*). Rev. Ecol. 53, 153–170.

Vitale, A.F., Tenucci, M., Papini, M., Lovari, S., 1986. Social behaviour of the calves of semi-wild Maremma cattle, Bos primigenius taurus. Appl. Anim. Behav. Sci. 16, 217–231. https://doi.org/10.1016/0168-1591(86)90115-2.

Vlasakker, Jvande, 2014. Bison Rewilding Plan, 2014–2024 — Rewilding Europe. Rewilding Europe, The Netherlands.

Wasserman, S., Faust, K., 1994. Social Network Analysis: Methods and Applications. Cambridge University Press.

Wey, T., Blumstein, D.T., Shen, W., Jordán, F., 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim. Behav. 75, 333–344.

Whitehead, H., 2009. SOCPROG programs: analysing animal social structures. Behav. Ecol. Sociobiol. 63, 765–778. https://doi.org/10.1007/s00265-008-0697-y.

Wiszniewski, J., Lusseau, D., Möller, L.M., 2010. Female bisexual kinship ties maintain social cohesion in a dolphin network. Anim. Behav. 80, 895–904. https://doi.org/10.1016/j.anbehav.2010.08.013.

Wright, J., 1998. Helping-at-the-nest and group size in the Arabian Babbler Turdoides squamiceps. J. Avian Biol. 105–112.

Wróblewski, K., 1927. Żubr Puszczy Bialowieskiej: monografja.