




Social network analysis of small social groups: Application of a hurdle GLMM approach in the Alpine marmot (*Marmota marmota*)

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Abstract

Social network analysis (SNA) has recently emerged as a fundamental tool to study animal behavior. While many studies have analyzed the relationship between environmental factors and behavior across large, complex animal populations, few have focused on species living in small groups due to limitations of the statistical methods currently employed. Some of the difficulties are often in comparing social structure across different sized groups and accounting for zero-inflation generated by analyzing small social units. Here, we use a case study to highlight how Generalized Linear Mixed Models (GLMMs) and hurdle models can overcome the issues inherent to study of social network metrics of groups that are small and variable in size. We applied this approach to study aggressive behavior in the Alpine marmot (*Marmota marmota*) using an eight-year long dataset of behavioral interactions across 17 small family groups (7.4 ± 3.3 individuals). We analyzed the effect of individual and group-level factors on aggression, including predictors frequently inferred in species with larger groups, as the closely related yellow-bellied marmot (*Marmota flaviventris*). Our approach included the use of hurdle GLMMs to analyze the zero-inflated metrics that are typical of aggressive networks of small social groups. Additionally, our results confirmed previously reported effects of dominance and social status on aggression levels, thus supporting the efficacy of our approach. We found differences between males and females in terms of levels of aggression and on the roles occupied by each in agonistic networks that were not predicted in a socially monogamous species. Finally, we provide some perspectives on social network analysis as applied to small social groups to inform subsequent studies.

KEYWORDS

aggression, GLMMs, small social groups, social network analysis, sociality, zero-inflated measures

Matteo Panaccio and Caterina Ferrari contributed equally to this paper.

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1 | INTRODUCTION

In social species, individuals live together and interact for a range of purposes, for example to facilitate reproduction (Schülke et al., 2010) and to increase foraging efficiency (Cassini, 1991) and predator avoidance (Ebensperger & Blumstein, 2006). Social structure results from behavioral interactions at the individual level (Whitehead, 2008). Such interactions with other group members can result in complex social structure at both the group and population level (Krause et al., 2007; Sih et al., 2009). Social network analysis (SNA) is a powerful analytical tool originally developed in sociology (Wasserman & Faust, 1994) and largely extended in recent years in the fields of ecology and animal behavior (Croft et al., 2011; Krause et al., 2007; Sih et al., 2009; Wey et al., 2008). A social network-based approach allows the quantification of social structure at every level, from individual to community (Farine & Whitehead, 2015). Furthermore, it is possible to analyze relationships between environmental and social factors and various types of social interactions in animal communities (Farine & Whitehead, 2015; Krause et al., 2009; Wey et al., 2008). Applications of this approach have included the study of disease or information spread within a population (Hamede et al., 2009), the study of population dynamics (Pinter-Wollman et al., 2013) and the evaluation of the relationship between the physical environment and social structure (Pinter-Wollman, 2015). With this approach, it is also possible to analyze the effect of the social environment on individual behavior within a social group (Maldonado-Chaparro et al., 2015; Wey & Blumstein, 2010) and on reproduction (Cameron et al., 2009; Wey & Blumstein, 2012).

A social network is a description of the social structure resulting from relationships between individuals that compose the system (Farine & Whitehead, 2015). The network is represented by a diagram comprising nodes, generally representing the individuals, and edges, showing relationships existing among the individuals (Krause et al., 2009; Whitehead, 2008). Relationships between social structure and focal variables can be studied by the deployment of social network metrics, which allow the characterization of node properties within the entire social system (Farine & Whitehead, 2015).

Social network analysis can be particularly useful when analyzing agonistic interactions (Whitehead, 2008). In a large number of animal species, agonistic interactions among individuals are needed to obtain or maintain the dominance status (Chase, 1982; Collias, 1944). Indeed, in many species, the dominant position guarantees exclusive access to reproductive partners (Barash, 1976). However, aggressive interactions are costly (Briffa & Sneddon, 2007; Marchant et al., 1995) because of their energetic cost (e.g., Hack, 1997) or risk of injuries or death (e.g., Ferrari et al., 2012). Individuals must therefore balance their aggression in a cost-benefit scenario, for instance triggering aggression under specific conditions or during a key period of time (e.g., Andino et al., 2011). Aggressive interactions will then be modulated based on individual (Sosa, 2016; Wey & Blumstein, 2010) and

social group (Maldonado-Chaparro et al., 2015) level factors, such as sex, age, dominance, group size, and sex ratio.

Despite the strengths of SNA, this approach is infrequently used to study small social groups. Indeed, several challenges are present in applying social network theory to groups with very few individuals. In animals that live in small social groups social network metrics can be unreliable (Silk et al., 2015) and are often zero-inflated, that is, present an over excess of zeros. If not correctly modeled, zero-inflation can invalidate the distributional assumptions of the analysis and alter the integrity of the inferences (Tu, 2006). An excess of zeros could be present especially in metrics resulting from analysis of agonistic behaviors due, for example, to individuals that do not interact with others. Indeed, in certain species, aggression rates are lower in smaller groups (Shen et al., 2014), for example when there are fewer competitors in the hierarchy (Alexander, 1974). In small groups of closely-related individuals such as the Alpine marmot (*Marmota marmota*), some individuals do not interact aggressively with others for several reasons, for example subordinates could avoid competing for dominant positions as they assume the role of helpers and contribute to the care of the offspring (Allainé, 2000). In addition, in groups with a high frequency of dispersal, marginal individuals may not interact aggressively with other group members due to a lack of opportunity. In such small groups, frequencies of performed aggressive interactions within dyads could therefore easily have a disproportionate number of zeros. In a small social group, the relative importance of an individual with a zero Social Network metric is higher than in a larger group, which could cause a bias in the results. Therefore, correctly addressing zero-inflation of aggression metrics is fundamental in analyzing social networks for small social groups. Furthermore networks with a different number of nodes (i.e., social groups of different size) can be challenging to compare (Croft et al., 2008).

Here, we applied methods more frequently used in larger social groups with adjustments that allow for comparison between multiple small groups of differing size. We used this method to test predictions on the effect of individual and group characteristics on agonistic behavior in Alpine marmots (*Marmota marmota*), a species characterized by living in stable small family groups (Barash, 1976). We tested the well-known positive relationship between dominance and aggression (e.g., Sosa, 2016; Turner et al., 2018) to support the efficacy of these methods. In addition, we tested for sex differences in the tendency to perform aggressive behavior; this is generally performed more frequently by males (e.g., Sosa, 2016) but this relationship is dependent on the social system (Magurran & Garcia, 2000). In the yellow-bellied marmot (*Marmota flaviventris*), a closely related species with a similar social system, sex differences are indeed absent (Wey & Blumstein, 2010) while in Alpine marmot sex differences in aggressive behavior have not previously been investigated. We therefore predicted individuals with higher dominance level would initiate the most aggressive interactions and that no sex differences in levels of performed aggression would be found in Alpine marmots.

2 | METHODS

2.1 | Subjects and data collection

The Alpine marmot is a highly social and territorial burrow-dwelling rodent that lives in high alpine and subalpine meadows in Europe. This species lives in social groups formed by 2–20 individuals, a dominant pair and their offspring (Allainé, 2000; Barash, 1989), with a cooperative breeding system. The status of dominance is reached and maintained both for males and females by the victory in aggressive interactions with other group members (Barash, 1976). Dominants reproduce almost exclusively (Barash, 1976; Cohas et al., 2007) and helpers delay dispersal to increase pups' survival (Allainé & Theuriau, 2004) and help with territory defense (Pasquaretta et al., 2015). The territory of an Alpine marmot group is relatively small and stable (Pasquaretta et al., 2012), thus they are easy to observe. A social group shares the same burrow system in which they hibernate socially during winter (Zelenka, 1965); burrows are also used overnight and to escape from predators (Ferrari et al., 2010).

This research project was conducted in Valsavarenche, Aosta, in the Gran Paradiso National Park, North-Western Italian Alps, 45°34' N, 7°11' E. The ongoing long-term project on Alpine marmots started in 2006. The study area is divided into two sites with different environmental conditions. The first area is at an altitude from 2100 m to 2280 m above sea level and is characterized by alpine meadows with extended rocky areas, at the upper limit of a mixed conifer forest. The second study area is at an altitude from 2220 m to 2430 m above sea level and is characterized by an open alpine meadow.

Data used in this analysis were collected over an eight year period (2010–2018). During this time span, 335 marmots belonging to 17 different familial groups (7 in the lower area and 10 in the upper area) were captured and marked with colored ear tags, thus were visually recognizable during social behavioral observations. We estimate that about 60% of all individuals of the studied families were marked and recognizable from a distance (65% of individuals aged 1 or more in 2018, 59% in 2017, 53% in 2016, in previous years we do not have data on the number of unmarked individuals).

Marmots were live-trapped every year from late April–May to mid-June (Ferrari et al., 2013). A second capture period was performed from mid-June to mid-July to capture pups immediately after their exit from the burrows. Animals were trapped with cages (Tomahawk Live Traps, Hazelhurst, WI, USA) with food baits. Once a marmot was trapped, two people transferred it to an opaque handling bag provided with a tear opening to access the animal's ears. These operations were performed for each captured marmot as a part of a standard protocol for captures, marking and data collection (see Ferrari et al., 2013), and required two or three operators.

Marmots were marked with a permanent transponder inserted under the skin in the scapula region (Mod. Bayern Animal Coder, Bayer S.p.a., Milan, Italy), and with a combination of two ear tags (Minirotag, 5 cm length, Ghislandi & Ghislandi, Bergamo, Italy) of six different colors. In pups and individuals for whom the application

of ear tags is not possible (e.g., injured ears), fur decoloration with atoxic cream (Modus bleach, Aosta, Italy) was performed. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of ISPRA (Higher Institute for Environmental Protection and Research, Protocol nr. 016970, April 2009) for captures of wild animals. We assessed marmot age based on weight, morphometric measures, and information from previous captures for individuals captured first as pups or juveniles. We divided age into three classes: pups (born during the summer), yearlings (1 year old), and adults (2 years old or more). Individuals were assigned to a known family if they shared the same burrow system.

2.2 | Behavioral data collection

Social behavioral observations were performed during most of the active season, from May to September, and during the entire active period (7 a.m. to 7 p.m.). In warmer months (July and August), observations were generally stopped from 12 p.m. to 2 p.m. due to very low observed activity of the animals (Ferrari & Panaccio, personal observation). Observations were performed evenly throughout the season and with a fixed schedule to ensure the same number of hours of observation (from 20 to 35 per year depending on the number of operators) was carried out for each familiar group and to cover all active hours of the day and the entire active season. We completed a total of 1769 hr of observations, with a mean of 193 ± 93 total hours per year.

Observations were performed at a distance of 50–100 meters so as not to interfere with normal behavior, using binoculars to detect animals and a scope for identification (Swaroski 30 × 75 and Nikon ED82 25–56 × 82). All occurrence scan sampling (Altmann, 1974) was used to record social interactions. Each family was observed non-stop for a 1-hr period (i.e., a scan) from the best position to observe the entire home range of the focal family. Individuals were generally not visible for the entire scan, as they spend time below ground or could be out of sight. Therefore, some missing observations are present, but with a low frequency for above-ground behaviors, as a large majority of the home range (we estimate a 70%–90% of it in each family) was generally visible from the observation point (Pasquaretta et al., 2012).

During the scan, all types of social behavior were recorded when at least one marked individual was involved. Observed behaviors were categorized as: agonistic, affiliative (both greeting and grooming behaviors), and play (Johns & Armitage, 1979), but only aggressive interactions were analyzed in this study. Aggression was defined according to Perrin et al. (1993). We recorded the ID of the initiator and recipient of the interaction and the winner. The winner was determined as the individual that blocks the other on the ground or makes him flee. The intensity of the aggression (presence/absence of physical contact and chasing) was also recorded, but was not used in this study. Table 1 provides the explanation of coded aggressive

Behavior code	Behavior coded as 1	Behavior coded as 0
C1	Individual that starts the interaction	Individual that does not start the interaction
C2	Individual attacks during aggression	Individual does not attack
C3	Individual that wins	Individual that loses (if unclear 0 to both)
C4	Chase the other	Does not chase
C5	In his own home range	Outside his own home range
C6	Aggressive (physical contact and bites)	Not aggressive

TABLE 1 Explanation of coded aggressive behaviors recorded in observations

behavior we recorded in our observations. An ethogram with full explanations for all coded behaviors is provided as Appendix S1.

2.3 | Construction of social networks

We built agonistic social networks for all the families that included at least three marked individuals in every year of the study for a total of 17 families. Individuals were included in the analysis if they were observed in at least five scans. We calculated interaction rates for aggressive behavior for each combination of two marked individuals within each family group within each year.

To account for missing observations (which occurred in our study as a result of our sampling protocol), association indices are frequently used in network studies, mostly to avoid false negatives (Farine & Whitehead, 2015). However, we used raw interaction rates here for four main reasons. (a) Aggressive interactions were recorded mostly during sampling periods, as we were able to observe a large majority of the home ranges (see par. 2.2) and aggressive behaviors were immediately obvious as they were often accompanied by vocalizations. (b) Asymmetry of the interactions was fundamental as our aim was to analyze performed and received aggression; the most appropriate association index to account for any missing observations occurring as a result of our sampling protocol, the Simple Ratio Index (Cairns & Schwager, 1987), has been developed for undirected networks and thus loses directionality of interactions. (c) 40% of social network studies use raw durations or frequencies of interactions (Webber & Vander Wal, 2019), as did a similar study in a related species, the yellow-bellied marmot (Wey & Blumstein, 2010).

For each individual, the asymmetric interaction rate with another group member was calculated as the number of performed aggressive interactions divided by the total number of hours of observations for that dyad (Whitehead, 2008). We considered aggressions initiated by each individual in the dyad separately, resulting in a directed social network (Wey et al., 2008). Interaction rates obtained were used to build an adjacency $N \times N$ matrix, where N is the number of individuals in the social group and each cell contains the interaction rate for that dyad. The initiator of the interaction appears on the rows and the receiver on the columns. Separate social networks for each group and for each year were inferred from their respective interaction matrices using the package *igraph* (Csardi & Nepusz, 2006) in R v.3.5.1. (R Core

Team, 2018). David's score (Gammell et al., 2003) was used to calculate the dominance level of each individual based on the outcomes of agonistic interactions, using the package *steepness* (de Vries et al., 2006) in R v.3.5.1. (R Core Team, 2018).

2.4 | Statistical analysis

Network metrics represent statistical measures used to characterize properties of individuals (nodes) or the whole network (Farine & Whitehead, 2015; Whitehead, 2008). We calculated the following social network metrics: degree (Newman, 2003), strength (Barthélemy et al., 2005), and eigenvector centrality (Newman, 2004), using the directed versions. Unweighted degree quantifies the number of other group members that interact with the focal individual (Sosa et al., 2020) and is divided into out-degree (to how many others interactions are performed) and in-degree (from how many others interactions are received). Strength is the sum of the weights of every interaction in which the focal individual is involved (Sosa et al., 2020), and is divided into out-strength (only initiated interactions) and in-strength (only received interactions). Eigenvector centrality measures the relative importance of an individual in the network (Newman, 2004). A brief description of the metrics is provided in Table 2. We calculated degree and strength metrics using the *tnet* package (Opsahl, 2009) and directed eigenvector centrality with the *igraph* package in R v.3.5.1. (R Core Team, 2018).

We modelled the relationship between individual characteristics and each social network metric as response variables using Generalized Linear Mixed Models (GLMMs) to take account of repeated measures on the same individuals and to avoid pseudoreplication (Crawley, 2007; Van De Pol & Wright, 2008). As GLMMs can handle unbalanced data (Pinheiro, 2014), we could take into account the differences in size among groups and among years by including individual, social group and year in the random structure of our model. We used this mixed-model approach in our study to investigate how sex, dominance, group size, and other factors affect aggressive interactions within the social group. For out-degree, in-degree, and eigenvector centrality metrics, we performed GLMMs with the *glmer* function in the *lme4* package (Bates et al., 2015) in R.

Strength metrics for aggressive interactions in our datasets presented zero-inflation, as a possible consequence of small group size and social system (see par.1). Indeed, zeros accounted for 24%

TABLE 2 Social network metrics used in our study

Metric	Description
Degree	The degree measures the number of links of a node, that is, the number of other individuals to whom the focal individual is connected. It is a basic but fundamental measure to analyze connection between sociality and individuals. For instance, it specifies the number of competitors of a dominant male, as the number of individuals that interact aggressively with him
Strength	Strength (or weighted degree) is the sum of links' weights in a weighted network, that is, the sum of the weight of all the interactions in which the focal individual is involved. This metric quantify the effect of interactions from or toward other group members
Eigenvector centrality	Eigenvector centrality is the first non-negative eigenvector value obtained by transforming an adjacency matrix linearly. It is a centrality measure that quantify the importance of a node within the social group. Its value is between 0 and 1, where 1 value represent individuals that gives stability to group and their removal have a large negative effect. This measures specify individuals with a great importance in affiliative or agonistic networks, and can be used for example to rank individuals in a network, such that they have higher values both if they interact with many individuals or if they have stronger interactions with few individuals

of out-strengths values and 21% of in-strength values. To address zero-inflation in these metrics, we used hurdle models (Pinheiro & Bates, 1995); here, the two processes generating the zeros and the positive values are separated, thus the probability of observing a zero is independent of the mean of the response variable. The hurdle models model the data with two separate equations: a binomial model that analyzes the likelihood for the response value to have a value of zero, and a linear model that is then applied to non-zero values in the response variable. The binomial probability model governs the binary outcome of whether the variable has a zero or a positive realization. If the realization is positive, the conditional distribution of the positives is governed by a truncated-at-zero model (Mullahy, 1986). A GLMM rather than a simple linear model is used to model the positive values, while accounting for repeated measures.

The distribution of the errors of the response variables for positive values of strength metrics was lognormal. For in-strength and out-strength, we therefore applied hurdle GLMMs using the *mixed_model* function with the *hurdle.lognormal* family in *GLMMadaptive* package (Rizopoulos, 2019) in R. Dorning and Harris (2019) used hurdle GLMMs to study the duration of encounters between red foxes (*Vulpes vulpes*), but to the best of our knowledge this is the first application of hurdle GLMMs to analyze social network metrics as a response variable.

The fixed factors analyzed in models for all network metrics were sex, social status, dominance index, group size (total number and number of adults), sex ratio (n males/ n females), presence of pups, and study site. Social status was a combination of age class and social status (subadult, subordinate adult, and dominant adult) to avoid correlation as dominants are always adults. Exact age was not used due to several missing values (individuals that were captured as adults of unknown age). Status and David's score were both included (with their correlation being tested in each model) as status was not inferred by the analysis of winner/loser in aggressive interactions, but was determined based upon whether or not they

bred. We calculated the Variance Inflation Factor (VIF) to test for collinearity in the fixed factors in each model by means of the *performance* package (Lüdtke et al., 2020). We considered VIF values < 5 to reflect relatively low collinearity among fixed factors, and VIF-values higher than 10 to indicate strong collinearity (Stine, 1995). We included individual ID to control for repeated measurements of same individuals, and family (group ID) to account for dependency due to membership of the same group (family), as random factors in our models.

For each network metric, we built different hurdle models and the best ones were selected by the Akaike Information Criterion (AIC, Akaike, 1974). The candidate model with the lowest AIC was chosen as the best model, together with the second lowest if they presented a delta AIC ≤ 2 , thus indicating substantial statistic support (Burnham & Anderson, 2002).

We used a permutation procedure to test the statistical significance of all predictors. For each of the 41 social networks, we built 1,000 permuted networks, that is 41,000 networks in total, and re-ran the models using the relevant set of permuted networks to obtain a 95% Confidence Interval for the model estimates. Any predictor which fell outside of this CI was deemed significant ($p < .05$). Permutations were performed with *rmperm* in *sna* package (Butts, 2008).

All data used in our study (collected data and calculated network metrics) are provided in the following repository: Panaccio, Matteo (2020), "Alpine marmot in GPNP: data for SNA of small social groups," Mendeley Data, V1, <https://doi.org/10.17632/d6xr82b856.1>.

3 | RESULTS

In the study population, group size varied from 2 to 16 individuals, with a mean and standard deviation of 7.4 ± 3.3 individuals (adults were 4.2 ± 1.8) for both sexes (the sex ratio was 0.51). We observed

TABLE 3 Coefficients in best models

SN Measure	Intercept	Sex.M	Status Subad.	Status Subad.	Status Subord.	David's score	Group size (adults)	Sex.ratio (M/F)	Presence of pups	Study site
Out-degree	0.342 ± 0.124	0.123 ± 0.14	-2.458 ± 0.716	-0.034 ± 0.152	0.176 ± 0.046	/	/	/	/	/
In-degree	-0.1723 ± 0.075	/	/	/	-0.122 ± 0.061	/	/	/	/	/
Out-strength zero	-1.877 ± 0.388	/	4.176 ± 0.995	0.188 ± 0.585	-0.729 ± 0.431	/	/	/	/	/
Out-strength	-1.97 ± 0.375	0.624 ± 0.171	/	/	0.127 ± 0.06	0.142 ± 0.046	-1.4167 ± 0.576	-0.301 ± 0.17	0.285 ± 0.165	/
In-strength zero	-0.916 ± 0.285	/	0.133 ± 0.739	-1.379 ± 0.739	0.056 ± 0.194	/	/	/	/	/
In-strength	-1.944 ± 0.309	/	/	/	-0.109 ± 0.076	0.034 ± 0.063	/	/	/	/
Eigenvector centrality	0.797 ± 0.067	0.146 ± 0.052	-0.258 ± 0.076	0.022 ± 0.056	/	-0.049 ± 0.014	/	/	/	/

Note: Estimates of coefficients (β) and standard errors of individual and social group factors on every social network measure. For strength and centrality measures are also reported coefficient for the zero part in the hurdle model. In gray relevant factors after permutation procedures ($p < .05$).

9,241 social interactions, of which 56.28% were affiliative (32.02% were grooming, 24.26% were greeting), 29.46% were play behavior and 14.26% (1,318) were agonistic. From the behavioral data, we built 43 social networks comprising a total of 91 individuals (13 of which were present across more than two years, 21 were present in two years and 57 were only present in one year). For each social network metric, we selected the best predictive model; the results are reported in Table 3. The Variance Inflation Factor showed a low correlation (< 5) for all predictors in the models. Individual ID always resulted as being the only random factor in the best fitting model, while familial group was never present.

Our models' results indicated a direct relationship between dominance index and both the total number of aggressive interactions performed and the number of individuals toward which aggression was directed (out-strength $\beta = 0.127 \pm 0.06$, see Figure 1; out-degree $\beta = 0.176 \pm 0.046$). Moreover, subadults were less likely than adults to initiate aggression toward any individual (out-strength zero $\beta = 4.176 \pm 0.995$) and generally performed aggressive interactions toward fewer other group members (out-degree $\beta = -2.458 \pm 0.716$).

Our results showed that aggressive interactions are performed more frequently by males than by females (out-strength: $\beta = 0.624 \pm 0.171$, see Figure 2), but the level of received interactions does not appear to show differences between the sexes (as this factor does not appear in the best models). Moreover, males had a higher centrality (eigenvector: $\beta = 0.146 \pm 0.052$), confirming their primary role in aggression networks.

We also found that the presence of pups reduces aggression within the group (out-strength $\beta = -0.301 \pm 0.17$), and we reported that in the open meadow site aggression levels were higher than in the mixed environment site (out-strength $\beta = 0.285 \pm 0.165$). All results were validated through permutation procedures, whose results are reported in Table 4.

4 | DISCUSSION

4.1 | Hurdle GLMM models for social network analysis

In our study, we only considered individuals observed in at least five different scan periods (number of observations ≥ 5 , as in a scan period there could be multiple observations). Our threshold was very low compared with other studies, for instance Aplin et al. (2013) applied a threshold of at least 100 observations. However, studies on the yellow-bellied marmot (Wey & Blumstein, 2010, 2012) also considered five observations sufficient to include an individual in the analysis. In fact, thresholding should be considered on a case-by-case basis (Farine & Whitehead, 2015) and in our analysis we only used individual-based metrics, thus the impact of an incorrect measure, resulting from individuals with fewer datapoints, is less important than with network-based measures (Whitehead, 2008). Basically, our threshold's aim was to remove transient individuals that do not consistently belong to the social group.

FIGURE 1 Effect of dominance index on out-strength. Graph of the relationship between out-strength and dominance index (David's score) showing regression line. Out-strength was transformed into a logarithmic scale. Regression line for the model that excludes the outlier is shown as dashed line

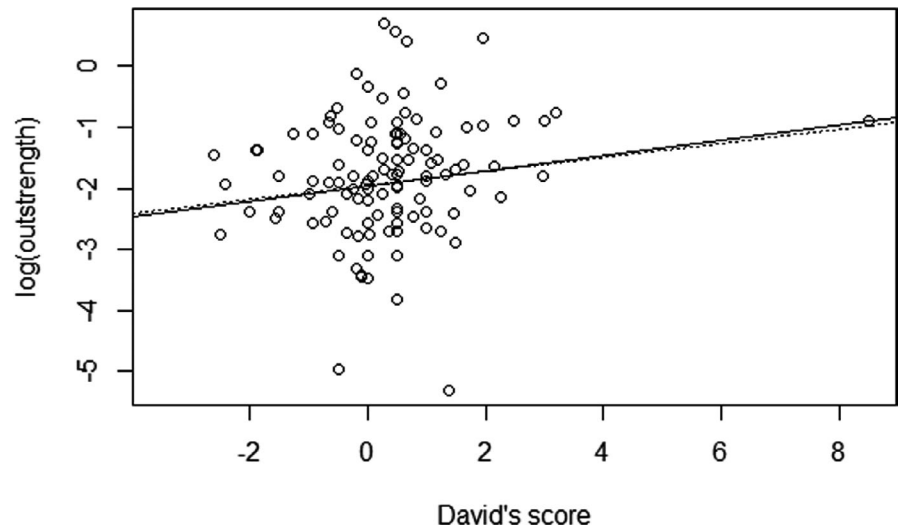


FIGURE 2 Effect of sex on out-strength. Boxplot of out-strength difference among sexes. Males performed more aggression than females ($\beta = 0.624$, $p < .001$)

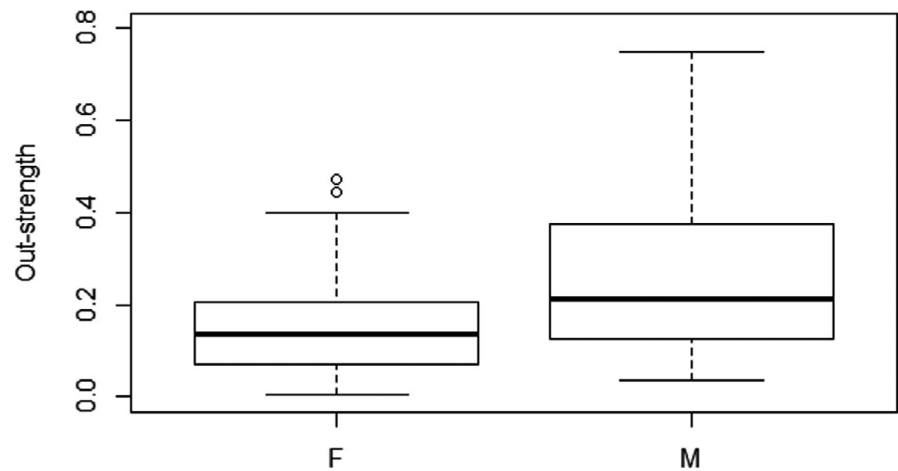


TABLE 4 Outcome of permutation procedures

Sn metric	Model fixed effect	Significance
Out-degree	Status of subadult	$p = .008$
	David's score	$p < .001$
In-degree	David's score	$p = .003$
Out-strength	Sex	$p < .001$
	David's score	$p = .01$
	Group size (adults)	$p < .001$
	Sex ratio	$p < .001$
	Presence of pups	$p = .01$
	Study site	$p = .009$
In-strength	David's score	$p = .006$
Eigenvector	Sex	$p < .001$
	Status of subordinate	$p = .002$
	Groups size (adults)	$p < .001$

Note: Significance of GLMMs results validated through permutation procedures.

The network metrics we selected, in particular degree and strength, have been demonstrated to be reliable measures in very small networks (Silk et al., 2015), while for eigenvector centrality,

reliability is less clear. However, studies such as Silk et al. (2015) do not consider zero-inflation in such analyzes, and this could have influenced the estimated reliability of these centrality metrics in small groups.

The use of hurdle models was the main adjustment we applied to social network analysis methods to use them in very small social groups. As far as we know, no other study has applied an SNA approach to groups of only seven individuals on average. In contrast, studies on yellow-bellied marmots considered groups of 20 individuals on average (Wey & Blumstein, 2010). Hurdle models permitted us to study these small groups, accounting for the zero-inflation that arose in our networks. Several group members indeed did not participate in any aggressive interactions in our dataset and network metrics therefore presented a disproportionate number of zeros. With a classic linear model, or GLMM in our case, zero inflation would have made the models invalid or highly inaccurate. These difficulties are indeed more likely in small groups, in which individuals that presented null SN metrics could have been excluded from the analysis with other approaches. We believe that the use of hurdle models is necessary mostly in studying aggressive interactions, which are more likely to present zero-inflated values, because in a very small group of closely related individuals several group members are likely

to not interact aggressively with others for kinship or dispersal reasons (Maldonado-Chaparro et al., 2015).

4.2 | Application in Alpine marmots

The application of our method to agonistic social networks allowed us to assess the effects of individual and social group characteristics on aggressive interactions within small social groups of a highly social rodent. The likelihood of initiating aggression was explained by both dominance index and social status, factors linked with an individual's chances of winning the interaction, and by sex.

In general, our results correctly fit into the traditional view of the cost-benefit balance inherent to aggressive behavior (Hamilton, 1964a, 1964b). In the Alpine marmot, the main benefit of the dominant status that is reached and maintained through more aggressive interactions toward conspecifics is the almost exclusive right to reproduction (Barash, 1976; Cohas et al., 2007). Risk of injuries or death is probably not an important cost of aggression as it occurs so infrequently (Ferrari et al., 2012). On the other hand, key costs could be the energetic and physiological effort of aggression. Indeed, oxygen consumption increases during fights (deCarvalho et al., 2004; Hack, 1997) and aggressive interactions reduce time that could be spent in foraging (Ancona et al., 2010). Therefore, during intense periods of fighting, energetic reserves of individuals could reduce (Higham et al., 2011; Low, 2006; Rovero et al., 2000). Besides, in more aggressive individuals the oxidative stress is higher (Costantini et al., 2008; Rammal et al., 2010); this was also demonstrated in our study population (Costantini et al., 2012).

Given these reasons, as the amounts of time and energy allocated to fighting depend on winning probabilities (Maynard Smith, 1974; Maynard Smith & Price, 1973); individuals with low chances of victory have an advantage in reducing their aggression, while individuals with a higher chance of victory will perform more aggressive interactions and are more likely to have a correspondingly higher reproductive success, as shown in yellow-bellied marmots (Huang et al., 2011; Wey & Blumstein, 2012). Yellow-bellied marmots share a similar overall group structure with the Alpine marmot, but with larger groups and a facultative cooperative breeding strategy (Blumstein & Armitage, 1999). Indeed, our results show that individuals with a higher dominance index initiate more aggressive interactions toward a larger number of other group members, confirming results in other species of social mammals (meerkats, *Suricata suricatta*: Madden et al., 2011; macaques, *Macaca sylvanus*: Sosa, 2016; spotted hyena, *Crocuta crocuta*: Turner et al., 2018). This suggests that for dominants the benefit of reproduction justifies costs associated with aggression, while in subordinates aggression is more limited as they cannot reach a dominant position. In the same way, subadults are very marginal in agonistic networks and they perform aggression toward far fewer individuals than do adults; this is consistent with results for yellow-bellied marmots (Wey & Blumstein, 2010). This is probably because one year old individuals have not yet reached

the physical strength to compete with adults (Mann et al., 1993). We were not able to include exact age in the analysis due to lack of data for many marmots first captured as adults, but we expect that in adults, older individuals would show higher levels of agonism. In fact, this tendency has been demonstrated in yellow-bellied marmots (Wey & Blumstein, 2010) and other mammals (Büttner et al., 2015). Dominance status frequently increases with age as competitive abilities improve (e.g., Verhulst et al., 2014), and in cooperatively breeding species, older subordinates usually take the place of dominants when they die (Wiley & Rabenold, 1984).

A major result of our study is that we found differences in aggression levels between males and females, while in *M. flaviventris* sex differences were not present (Wey & Blumstein, 2010). The yellow-bellied marmot is a harem-polygynous species, that is, one male defends one or more females (Armitage, 1991), while the Alpine marmot is monogamous (Barash, 1976; Perrin et al., 1993). Therefore, in *M. marmota* we also expected an absence of a sex difference that could also be more justified than in *M. flaviventris*. Indeed, aggression levels of both sexes are generally similar in monogamous species (Cole et al., 1980; Swenson, 1997) and female Alpine marmots also suppress subordinates' reproduction with continuous aggression (Hackländer et al., 2003). The higher concentration of testosterone in males, common in all species of mammals (e.g., Bermond et al., 1982; Edwards, 1969; Simon et al., 1985), cannot explain our results because there is no evidence, as far as we know, that in Alpine marmots testosterone level is relatively higher than in yellow-bellied marmots. A possible reason for our results could be the observed high turnover rates in dominant males (12) with respect to dominant female turnovers (6), and consequently a higher number of male-to-male aggressive interactions to reach dominant status. However, the absence of a sex difference in the yellow-bellied marmot, a matrilineal polygynous species (Armitage, 1991), underlines the necessity of further investigations.

On the other hand, received interactions do not show sex differences and this can perhaps be explained because of inter-sex aggression, a behavior also found in the yellow-bellied marmot (Armitage, 1974) and one that is frequently observed in our study population (we reported 37 cases out of 167 total aggressive interactions in year 2018 alone). Although an explanation for this behavior in marmots was not investigated here, inter-sex aggression with other group members could occur due to territoriality against dispersed individuals that become part of the group, sexual aggression among mating partners (King, 1973), or during intense territorial fights (each of these examples were observed during data collection). While females perform less aggression than males, a lack of difference in received interactions, that is in-degree and in-strength, could be explained by a higher male-to-female aggression (for females the lower rates of aggression received from other females are probably balanced by increased rates of aggression received from males). Indeed, in 2018 females received 36% of total aggression from males (20/57) while males received only 14% (17/123) of aggression from females.

The lower level of aggression that we found in groups with pups could be an effect of a higher investment in parental and

extra-parental care and a subsequent reduction in aggressive behaviors. However, the absence of pups in social groups could reveal the absence of a stable dominant pair (it could be for instance the result of infanticide by competitor males, as detected by Coulon et al., 1995), thus the higher level of aggressive behaviors could be explained by a higher level of competition for the dominant role.

Finally, the effect we reported due to study area could be explained by a couple of factors. In our site with more open areas home ranges appear to be smaller, maybe because of the higher quality of vegetation (C. Ferrari, unpublished data). Thus, a higher level of competition for dominance is more likely in the open site, while in the closed site the stability of the social group could be more important in defending a greater home range from neighbors. Furthermore, in the open site individuals spend less time in vigilance because predators can more easily be detected (Ferrari et al., 2010). Therefore, time spent in social interactions, even agonistic ones, could increase (Ferrari et al., in revision).

5 | CONCLUSIONS

We designed and trialled a method for analyzing small social groups of different sizes with an SNA approach. We applied adjustments to commonly used methods, including the use of hurdle GLMMs to analyze the zero-inflated metrics that are typical of aggressive networks of small groups. We highlighted an approach to examine a set of hypotheses to explain observed behavior and provided an example by analyzing the effects of individual and group characteristics on aggressive interactions initiated and received. Our study revealed novel results regarding the role of sex in aggressive interactions in Alpine marmots, including unexpected differences between males and females, thus highlighting the power of SNA based methods.

Our analysis provides a useful example for measuring sociality in small groups, which currently remains highly challenging in a context of SNA approaches. Accounting for zero-inflation of aggression metrics can indeed allow a more effective analysis of multiple smaller groups than by using a traditional modelling approach.

Further examinations of species with a social structure based on small stable family groups are needed to demonstrate the reliability of hurdle GLMMs for social network analysis. Our approach could be useful to test additional hypotheses about factors influencing social behavior in small social groups, including the effects of other individual and group level characteristics (e.g., personality) on social structure, or the effects of group-level patterns of aggressive/affiliative behavior on reproductive success.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest in this study.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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