

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

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

This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1880627> since 2022-11-25T12:16:52Z

Published version:

DOI:10.1111/eth.13151

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

1 **Social Network Analysis of small social groups: application of a**
2 **hurdle GLMMs approach in the Alpine marmot (*Marmota***
3 ***marmota*)**

4
5 Panaccio Matteo ^{1*}, Ferrari Caterina ^{2,3*}, Bassano Bruno ³, Stanley Christina R. ⁴ and von Hardenberg
6 Achaz ⁴

7
8 ¹ Dipartimento di Biologia e Biotechnologie, University of Pavia, Pavia, Italy

9 ² Dipartimento di Scienze della Vita e Biologia dei Sistemi, University of Turin, Torino, Italy

10 ³ Alpine Wildlife Research Centre, Gran Paradiso National Park, Valsavarenche (AO), Italy

11 ⁴ Conservation Biology Research Group, Department of Biological Sciences, University of Chester, Chester, United Kingdom

12 * These two authors contributed equally to this paper

13
14 **ACKNOWLEDGMENTS**

15 We thank Cristian Pasquaretta, Nicole Martinet, Martina Adorni, Elisabetta Delucchi, Marco Lucchesi and all other
16 students whose contribute in data collection was fundamental. We also thank Gran Paradiso park rangers Martino
17 Nicolino and Davide Glarey for their help in the field. Thanks to Prof L. Ebensperger, Dr. S. Sosa and an
18 anonymous referee for their useful suggestions that helped us to improve our submission.

19
20 **Conflict of interest**

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

22
23 **ABSTRACT**

24 Social Network Analysis (SNA) has recently emerged as a fundamental tool to study animal behavior.
25 While many studies have analyzed the relationship between environmental factors and behavior across
26 large, complex animal populations, few have focused on species living in small groups due to limitations
27 of the statistical methods currently employed. Some of the difficulties are often in comparing social
28 structure across different sized groups and accounting for zero-inflation generated by analyzing small
29 social units. Here we use a case study to highlight how Generalized Linear Mixed Models (GLMMs) and
30 hurdle models can overcome the issues inherent to study of social network metrics of groups that are
31 small and variable in size. We applied this approach to study aggressive behavior in the Alpine marmot
32 (*Marmota marmota*) using an eight-year long dataset of behavioral interactions across 17 small family
33 groups (7.4 ± 3.3 individuals). We analyzed the effect of individual and group-level factors on aggression,
34 including predictors frequently inferred in species with larger groups, as the closely related yellow-bellied
35 marmot (*Marmota flaviventris*). Our approach included the use of hurdle GLMMs to analyze the zero-
36 inflated metrics that are typical of aggressive networks of small social groups. Additionally, our results
37 confirmed previously reported effects of dominance and social status on aggression levels, thus

38 supporting the efficacy of our approach. We found differences between males and females in terms of
39 levels of aggression and on the roles occupied by each in agonistic networks that were not predicted in a
40 socially monogamous species. Finally, we provide some perspectives on social network analysis as
41 applied to small social groups to inform subsequent studies.

42

43 **KEYWORDS**

44 Social Network Analysis, sociality, aggression, GLMMs, small social groups, zero-inflated measures.

45

46

47 **1. INTRODUCTION**

48

49 In social species, individuals live together and interact for a range of purposes, for example to facilitate
50 reproduction (Schülke et al., 2010) and to increase foraging efficiency (Cassini, 1991) and predator
51 avoidance (Ebensperger & Blumstein, 2006). Social structure results from behavioral interactions at the
52 individual level (Whitehead, 2008). Such interactions with other group members can result in complex
53 social structure at both the group and population level (Krause, Croft, & James, 2007; Sih, Hanser, &
54 McHugh, 2009). Social network analysis (SNA) is a powerful analytical tool originally developed in
55 sociology (Wasserman & Faust, 1994) and largely extended in recent years in the fields of ecology and
56 animal behaviour (Croft, Madden, Franks, & James, 2011; Krause, Croft, & James, 2007; Sih, Hanser, &
57 McHugh, 2009; Wey, Blumstein, Shen, & Jordán, 2008). A social network-based approach allows the
58 quantification of social structure at every level, from individual to community (Farine & Whitehead,
59 2015). Furthermore, it is possible to analyze relationships between environmental and social factors and
60 various types of social interactions in animal communities (Farine & Whitehead, 2015; Krause, Lusseau,
61 & James, 2009; Wey, Blumstein, Shen, & Jordán, 2008). Applications of this approach have included the
62 study of disease or information spread within a population (Hamede, Bashford, McCallum, & Jones,
63 2009), the study of population dynamics (Pinter-Wollman et al., 2013) and the evaluation of the
64 relationship between the physical environment and social structure (Pinter-Wollman, 2015). With this
65 approach it is also possible to analyze the effect of the social environment on individual behaviour within
66 a social group (Maldonado-Chaparro, Hubbard, & Blumstein, 2015; Wey & Blumstein, 2010) and on
67 reproduction (Cameron, Setsaas, & Linklater, 2009; Wey & Blumstein, 2012).

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

74 SNA can be particularly useful when analyzing agonistic interactions (Whitehead, 2008). In a large
75 number of animal species, agonistic interactions among individuals are needed to obtain or maintain the
76 dominance status (Collias, 1944; Chase, 1982). Indeed, in many species, the dominant position guarantees
77 exclusive access to reproductive partners (Barash, 1976). However, aggressive interactions are costly
78 (Briffa & Sneddon, 2007; Marchant, Mendl, Rudd, & Broom, 1995) because of their energetic cost (e.g.
79 Hack, 1997) or risk of injuries or death (e.g. Ferrari, Pasquaretta, von Hardenberg, & Bassano, 2012).
80 Individuals must therefore balance their aggression in a cost-benefit scenario, for instance triggering
81 aggression under specific conditions or during a key period of time (e.g. Andino et al., 2011). Aggressive
82 interactions will then be modulated based on individual (Sosa, 2016; Wey & Blumstein, 2010) and social
83 group (Maldonado-Chaparro et al., 2015) level factors, such as sex, age, dominance, group size and sex
84 ratio.

85 Despite the strengths of SNA, this approach is infrequently used to study small social groups. Indeed,
86 several challenges are present in applying social network theory to groups with very few individuals. In
87 animals that live in small social groups social network metrics can be unreliable (Silk et al., 2015) and are
88 often zero-inflated, i.e. present an over excess of zeros. If not correctly modeled, zero-inflation can
89 invalidate the distributional assumptions of the analysis and alter the integrity of the inferences (Tu,
90 2006). An excess of zeros could be present especially in metrics resulting from analysis of agonistic
91 behaviors due, for example, to individuals that do not interact with others. Indeed, in certain species,
92 aggression rates are lower in smaller groups (Shen, Akçay, & Rubenstein, 2014), for example when there
93 are fewer competitors in the hierarchy (Alexander, 1947). In small groups of closely-related individuals
94 such as the Alpine marmot (*Marmota marmota*), some individuals do not interact aggressively with
95 others for several reasons, for example subordinates could avoid competing for dominant positions as
96 they assume the role of helpers and contribute to the care of the offspring (Allainé, 2000). In addition, in
97 groups with a high frequency of dispersal, marginal individuals may not interact aggressively with other
98 group members due to a lack of opportunity. In such small groups frequencies of performed aggressive
99 interactions within dyads could therefore easily have a disproportionate number of zeros. In a small social
100 group, the relative importance of an individual with a zero Social Network metric is higher than in a
101 larger group, which could cause a bias in the results. Therefore, correctly addressing zero-inflation of
102 aggression metrics is fundamental in analyzing social networks for small social groups. Furthermore
103 networks with a different number of nodes (i.e. social groups of different size) can be challenging to
104 compare (Croft, 2008).

105 Here we applied methods more frequently used in larger social groups with adjustments that allow for
106 comparison between multiple small groups of differing size. We used this method to test predictions on
107 the effect of individual and group characteristics on agonistic behaviour in Alpine marmots (*Marmota*
108 *marmota*), a species characterized by living in stable small family groups (Barash, 1976). We tested the
109 well-known positive relationship between dominance and aggression (e.g. Sosa, 2016; Turner, Bills &
110 Holekamp, 2018) to support the efficacy of these methods. In addition we tested for sex differences in the

111 tendency to perform aggressive behavior; this is generally performed more frequently by males (e.g. Sosa,
112 2016) but this relationship is dependent on the social system (Magurran & Garcia, 2000). In the yellow-
113 bellied marmot (*Marmota flaviventris*), a closely related species with a similar social system, sex
114 differences are indeed absent (Wey & Blumstein, 2010) while in Alpine marmot sex differences in
115 aggressive behaviour have not previously been investigated. We therefore predicted individuals with
116 higher dominance level would initiate the most aggressive interactions and that no sex differences in
117 levels of performed aggression would be found in Alpine marmots.

118

119

120 **2. METHODS**

121

122 **2.1 Subjects and data collection**

123 The Alpine marmot is a highly social and territorial burrow-dwelling rodent that lives in high alpine and
124 subalpine meadows in Europe. This species lives in social groups formed by 2-20 individuals, a dominant
125 pair and their offspring (Allainé, 2000; Barash, 1989), with a cooperative breeding system. The status of
126 dominance is reached and maintained both for males and females by the victory in aggressive interactions
127 with other group members (Barash, 1976). Dominants reproduce almost exclusively (Barash, 1976;
128 Cohas, Yoccoz, & Allainé, 2007) and helpers delay dispersal to increase pups' survival (Allainé &
129 Theuriau, 2004) and help with territory defense (Pasquaretta et al., 2015). The territory of an Alpine
130 marmot group is relatively small and stable (Pasquaretta et al., 2012) thus they are easy to observe. A
131 social group shares the same burrow system in which they hibernate socially during winter (Zelenka,
132 1965); burrows are also used overnight and to escape from predators (Ferrari, Bogliani, & von
133 Hardenberg, 2010).

134 This research project was conducted in Valsavarenche, Aosta, in the Gran Paradiso National Park, North-
135 Western Italian Alps, 45°34' N, 7°11' E. The ongoing long-term project on Alpine marmots started in
136 2006. The study area is divided into two sites with different environmental conditions. The first area is at
137 an altitude from 2100 m to 2280 m above sea level and is characterized by alpine meadows with extended
138 rocky areas, at the upper limit of a mixed conifer forest. The second study area is at an altitude from 2220
139 m to 2430 m above sea level and is characterized by an open alpine meadow.

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

146 Marmots were live-trapped every year from late April-May to mid June (Ferrari et al., 2013). A second
147 capture period was performed from mid-June to mid-July to capture pups immediately after their exit

148 from the burrows. Animals were trapped with cages (Tomahawk Live Traps, Hazelhurst, WI, USA) with
149 food baits. Once a marmot was trapped, two people transferred it to an opaque handling bag provided
150 with a tear opening to access the animal's ears. These operations were performed for each captured
151 marmot as a part of a standard protocol for captures, marking and data collection (see Ferrari et al. ,
152 2013), and required two or three operators.

153 Marmots were marked with a permanent transponder inserted under the skin in the scapula region (Mod.
154 Bayern Animal Coder, Bayer S.p.a., Milan, Italy), and with a combination of two ear tags (Minirotag, 5
155 cm length, Ghislandi & Ghislandi, Bergamo, Italy) of six different colors. In pups and individuals for
156 whom the application of ear tags is not possible (e.g. injured ears), fur decoloration with atoxic cream
157 (Modus bleach, Aosta, Italy) was performed. All applicable international, national, and/or institutional
158 guidelines for the care and use of animals were followed. All procedures performed in studies involving
159 animals were in accordance with the ethical standards of ISPRA (Higher Institute for Environmental
160 Protection and Research, Protocol nr. 016970, April 2009) for captures of wild animals. We assessed
161 marmot age based on weight, morphometric measures and information from previous captures for
162 individuals captured first as pups or juveniles. We divided age into three classes: pups (born during the
163 summer), yearlings (1 year old) and adults (2 years old or more). Individuals were assigned to a known
164 family if they shared the same burrow system.

165

166 **2.2 Behavioral data collection**

167 Social behavioral observations were performed during most of the active season, from May to September,
168 and during the entire active period (7am to 7pm). In warmer months (July and August), observations were
169 generally stopped from 12pm to 2pm due to very low observed activity of the animals (Ferrari et al., 2020
170 in revision). Observations were performed evenly throughout the season and with a fixed schedule to
171 ensure the same number of hours of observation (from 20 to 35 per year depending on the number of
172 operators) was carried out for each familiar group and to cover all active hours of the day and the entire
173 active season. We completed a total of 1769 hours of observations, with a mean of 193 ± 93 total hours
174 per year.

175 Observations were performed at a distance of 50-100 meters so as not to interfere with normal behavior,
176 using binoculars to detect animals and a scope for identification (Swaroski 30x75 and Nikon ED82 25-
177 56x82). All occurrence scan sampling (Altmann, 1974) was used to record social interactions. Each
178 family was observed nonstop for a one-hour period (i.e. a scan) from the best position to observe the
179 entire home range of the focal family. Individuals were generally not visible for the entire scan, as they
180 spend time below ground or could be out of sight. Therefore some missing observations are present, but
181 with a low frequency for above-ground behaviors, as a large majority of the home range (we estimate a
182 70-90% of it in each family) was generally visible from the observation point (Pasquaretta et al. , 2012).

183 During the scan, all types of social behavior were recorded when at least one marked individual was
184 involved. Observed behaviors were categorized as: agonistic, affiliative (both greeting and grooming

185 behaviors) and play (Johns & Armitage 1979), but only aggressive interactions were analysed in this
186 study. Aggression was defined according to Perrin, Coulon & Le Berre (1993). We recorded the ID of the
187 initiator and recipient of the interaction and the winner. The winner was determined as the individual that
188 blocks the other on the ground or makes him flee. The intensity of the aggression (presence/absence of
189 physical contact and chasing) was also recorded, but was not used in this study. Table 1 provides the
190 explanation of coded aggressive behavior we recorded in our observations. An ethogram with full
191 explanations for all coded behaviors is provided as supplementary material S.1.

192

193 **2.3 Construction of social networks**

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

198 To account for missing observations (which occurred in our study as a result of our sampling protocol),
199 association indices are frequently used in network studies, mostly to avoid false negatives (Farine &
200 Whitehead, 2015). However, we used raw interaction rates here for four main reasons. (1) Aggressive
201 interactions were recorded mostly during sampling periods, as we were able to observe a large majority of
202 the home ranges (*see par. 2.2.*) and aggressive behaviors were immediately obvious as they were often
203 accompanied by vocalisations. (2) Asymmetry of the interactions was fundamental as our aim was to
204 analyze performed and received aggression; the most appropriate association index to account for any
205 missing observations occurring as a result of our sampling protocol, the Simple Ratio Index (Cairns &
206 Schwager, 1987), has been developed for undirected networks and thus loses directionality of
207 interactions. (3) 40% of social network studies use raw durations or frequencies of interactions (Webber
208 & Vander Wal, 2019), as did a similar study in a related species, the yellow-bellied marmot (Wey &
209 Blumstein, 2010).

210 For each individual the asymmetric interaction rate with another group member was calculated as the
211 number of performed aggressive interactions divided by the total number of hours of observations for that
212 dyad (Whitehead, 2008). We considered aggressions initiated by each individual in the dyad separately,
213 resulting in a directed social network (Wey & Blumstein, 2008). Interaction rates obtained were used to
214 build an adjacency $N \times N$ matrix, where N is the number of individuals in the social group and each cell
215 contains the interaction rate for that dyad. The initiator of the interaction appears on the rows and the
216 receiver on the columns. Separate social networks for each group and for each year were inferred from
217 their respective interaction matrices using the package *igraph* (Csardi & Nepusz, 2006) in R v.3.5.1. (R
218 core team, 2018). David's score (Gammell et al., 2003) was used to calculate the dominance level of each
219 individual based on the outcomes of agonistic interactions, using the package *steepness* (de Vries,
220 Stevens, & Vervaecke, 2006) in R v.3.5.1. (R core team, 2018).

221

222 2.4 Statistical analysis

223 Network metrics represent statistical measures used to characterize properties of individuals (nodes) or
224 the whole network (Farine & Whitehead, 2015, Whitehead, 2008). We calculated the following social
225 network metrics: degree (Newman, 2003), strength (Barthélemy, Barrat, Pastor-Satorras, & Vespignani,
226 2005) and eigenvector centrality (Newman, 2004), using the directed versions. Unweighted degree
227 quantifies the number of other group members that interact with the focal individual (Sosa, Sueur, &
228 Puga-Gonzalez, 2020) and is divided into out-degree (to how many others interactions are performed) and
229 in-degree (from how many others interactions are received). Strength is the sum of the weights of every
230 interaction in which the focal individual is involved (Sosa, Sueur, & Puga-Gonzalez, 2020), and is
231 divided into out-strength (only initiated interactions) and in-strength (only received interactions).
232 Eigenvector centrality measures the relative importance of an individual in the network (Newman, 2004).
233 A brief description of the metrics is provided in Table 2. We calculated degree and strength metrics using
234 the *tnet* package (Opsahl, 2009) and directed eigenvector centrality with the *igraph* package in R v.3.5.1.
235 (R core team, 2018).

236 We modelled the relationship between individual characteristics and each social network metric as
237 response variables using Generalized Linear Mixed Models (GLMMs) to take account of repeated
238 measures on the same individuals and to avoid pseudoreplication (Crawley, 2007; Van De Pol & Wright,
239 2008). As GLMMs can handle unbalanced data (Pinhero, 2014) we could take into account the
240 differences in size among groups and among years by including individual, social group and year in the
241 random structure of our model. We used this mixed-model approach in our study to investigate how sex,
242 dominance, group size and other factors affect aggressive interactions within the social group. For out-
243 degree, in-degree and eigenvector centrality metrics we performed GLMMs with the *glmer* function in the
244 *lme4* package (Bates, Mächler, Bolker & Walker, 2015) in R.

245 Strength metrics for aggressive interactions in our datasets presented zero-inflation, as a possible
246 consequence of small group size and social system (*see par.1*). Indeed zeros accounted for 24% of out-
247 strengths values and 21% of in-strength values. To address zero-inflation in these metrics we used hurdle
248 models (Pinheiro & Bates, 1995); here the two processes generating the zeros and the positive values are
249 separated, thus the probability of observing a zero is independent of the mean of the response variable.
250 The hurdle models model the data with two separate equations: a binomial model that analyzes the
251 likelihood for the response value to have a value of zero, and a linear model that is then applied to non-
252 zero values in the response variable. The binomial probability model governs the binary outcome of
253 whether the variable has a zero or a positive realization. If the realization is positive, the conditional
254 distribution of the positives is governed by a truncated-at-zero model (Mullahy, 1986). A GLMM rather
255 than a simple linear model is used to model the positive values, whilst accounting for repeated measures.
256 The distribution of the errors of the response variables for positive values of strength metrics was
257 lognormal. For in-strength and out-strength we therefore applied hurdle GLMMs using the *mixed_model*
258 function with the *hurdle.lognormal* family in *GLMMadaptive* package (Rizopoulos, 2019) in R. Dorning

259 & Harris (2019) used hurdle GLMMs to study the duration of encounters between red foxes (*Vulpes*
260 *vulpes*), but to the best of our knowledge this is the first application of hurdle GLMMs to analyze social
261 network metrics as a response variable.

262 The fixed factors analyzed in models for all network metrics were sex, social status, dominance index,
263 group size (total number and number of adults), sex ratio (n° males/ n° females), presence of pups and
264 study site. Social status was a combination of age class and social status (subadult, subordinate adult and
265 dominant adult) to avoid correlation as dominants are always adults. Exact age was not used due to
266 several missing values (individuals that were captured as adults of unknown age). Status and David's
267 score were both included (with their correlation being tested in each model) as status was not inferred by
268 the analysis of winner/loser in aggressive interactions, but was determined based upon whether or not
269 they bred. We calculated the Variance Inflation Factor (VIF) to test for collinearity in the fixed factors in
270 each model by means of the *performance* package (Lüdtke, Makowski, Waggoner & Patil, 2020). We
271 considered VIF values < 5 to reflect relatively low collinearity among fixed factors, and VIF-values
272 higher than 10 to indicate strong collinearity (Stine, 1995). We included individual ID to control for
273 repeated measurements of same individuals, and family (group ID) to account for dependency due to
274 membership of the same group (family), as random factors in our models.

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

279 We used a permutation procedure to test the statistical significance of all predictors. For each of the 41
280 social networks we built 1000 permuted networks, i.e. 41000 networks in total, and re-ran the models
281 using the relevant set of permuted networks to obtain a 95% Confidence Interval for the model estimates.
282 Any predictor which fell outside of this CI was deemed significant ($P < 0.05$). Permutations were
283 performed with *rmperm* in *sna* package (Butts, 2008).

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

287

288

289 3. RESULTS

290 In the study population group size varied from 2 to 16 individuals, with a mean and standard deviation of
291 7.4 ± 3.3 individuals (adults were 4.2 ± 1.8) for both sexes (the sex ratio was 0.51). We observed 9241
292 social interactions, of which 56.28% were affiliative (32.02% were grooming, 24.26% were greeting),
293 29.46% were play behavior and 14.26% (1318) were agonistic. From the behavioral data, we built 43
294 social networks comprising a total of 91 individuals (13 of which were present across more than two
295 years, 21 were present in two years and 57 were only present in one year). For each social network metric

296 we selected the best predictive model; the results are reported in table 3. The Variance Inflation Factor
297 showed a low correlation (< 5) for all predictors in the models. Individual ID always resulted as being the
298 only random factor in the best fitting model, while familial group was never present.
299 Our models' results indicated a direct relationship between dominance index and both the total number of
300 aggressive interactions performed and the number of individuals towards which aggression was directed
301 (out-strength $\beta = 0.127 \pm 0.06$, see Fig. 1; out-degree $\beta = 0.176 \pm 0.046$). Moreover, subadults were less
302 likely than adults to initiate aggression towards any individual (out-strength zero $\beta = 4.176 \pm 0.995$) and
303 generally performed aggressive interactions towards fewer other group members (out-degree $\beta = -2.458 \pm$
304 0.716).
305 Our results showed that aggressive interactions are performed more frequently by males than by females
306 (out-strength: $\beta = 0.624 \pm 0.171$, see Fig. 2), but the level of received interactions does not appear to show
307 differences between the sexes (as this factor does not appear in the best models). Moreover males had a
308 higher centrality (eigenvector: $\beta = 0.146 \pm 0.052$), confirming their primary role in aggression networks.
309 We also found that the presence of pups reduces aggression within the group (out-strength $\beta = -0.301 \pm$
310 0.17), and we reported that in the open meadow site aggression levels were higher than in the mixed
311 environment site (out-strength $\beta = 0.285 \pm 0.165$). All results were validated through permutation
312 procedures, whose results are reported in table 4.

313

314

315 **4. DISCUSSION**

316

317 **4.1 Hurdle GLMM models for social network analysis**

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

327 The network metrics we selected, in particular degree and strength, have been demonstrated to be reliable
328 measures in very small networks (Silk et al., 2015), whilst for eigenvector centrality, reliability is less
329 clear. However, studies such as Silk et al. (2015) do not consider zero-inflation in such analyzes, and this
330 could have influenced the estimated reliability of these centrality metrics in small groups.

331 The use of hurdle models was the main adjustment we applied to Social Network Analysis methods to use
332 them in very small social groups. As far as we know, no other study has applied an SNA approach to

333 groups of only seven individuals on average. In contrast, studies on yellow-bellied marmots considered
334 groups of 20 individuals on average (Wey & Blumstein, 2010). Hurdle models permitted us to study these
335 small groups, accounting for the zero-inflation that arose in our networks. Several group members indeed
336 did not participate in any aggressive interactions in our dataset and network metrics therefore presented a
337 disproportionate number of zeros. With a classic linear model, or GLMM in our case, zero inflation
338 would have made the models invalid or highly inaccurate. These difficulties are indeed more likely in
339 small groups, in which individuals that presented null SN metrics could have been excluded from the
340 analysis with other approaches. We believe that the use of hurdle models is necessary mostly in studying
341 aggressive interactions, which are more likely to present zero-inflated values, because in a very small
342 group of closely related individuals several group members are likely to not interact aggressively with
343 others for kinship or dispersal reasons (Maldonado-Chaparro, Hubbard, & Blumstein, 2015).

344

345 **4.2 Application in Alpine marmots**

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

350 In general, our results correctly fit into the traditional view of the cost-benefit balance inherent to
351 aggressive behaviour (Hamilton, 1964a, 1964b). In the Alpine marmot, the main benefit of the dominant
352 status that is reached and maintained through more aggressive interactions towards conspecifics is the
353 almost exclusive right to reproduction (Barash, 1976, Cohas, Yoccoz, & Allainé, 2007). Risk of injuries
354 or death is probably not an important cost of aggression as it occurs so infrequently (Ferrari et al., 2012).
355 On the other hand, key costs could be the energetic and physiological effort of aggression. Indeed, oxygen
356 consumption increases during fights (deCarvalho, Watson, & Field, 2004; Hack, 1997) and aggressive
357 interactions reduce time that could be spent in foraging (Ancona, Drummond, & Zaldívar-Rae, 2010).
358 Therefore during intense periods of fighting, energetic reserves of individuals could reduce (Higham,
359 Heistermann, & Maestriperi, 2011; Low, 2006; Rovero, Hughes, Whiteley, & Chelazzi, 2000). Besides,
360 in more aggressive individuals the oxidative stress is higher (Costantini, Carere, Caramaschi, & Koolhaas,
361 2008; Rammal, Bouayed, & Soulimani, 2010); this was also demonstrated in our study population
362 (Costantini et al., 2012).

363 Given these reasons, as the amounts of time and energy allocated to fighting depend on winning
364 probabilities (Maynard-Smith, 1974; Maynard-Smith & Price, 1973); individuals with low chances of
365 victory have an advantage in reducing their aggression, whilst individuals with a higher chance of victory
366 will perform more aggressive interactions and are more likely to have a correspondingly higher
367 reproductive success, as shown in yellow bellied marmots (Huang, Wey & Blumstein, 2011; Wey &
368 Blumstein, 2012). Yellow-bellied marmots share a similar overall group structure with the Alpine
369 marmot, but with larger groups and a facultative cooperative breeding strategy (Blumstein & Armitage,

370 1999). Indeed, our results show that individuals with a higher dominance index initiate more aggressive
371 interactions towards a larger number of other group members, confirming results in other species of social
372 mammals (meerkats, *Suricata suricatta*: Madden, Drewe, Pearce, & Clutton-Brock, 2011; macaques,
373 *Macaca sylvanus*: Sosa, 2016; spotted hyena, *Crocuta crocuta*: Turner et al., 2018). This suggests that for
374 dominants the benefit of reproduction justifies costs associated with aggression, whilst in subordinates
375 aggression is more limited as they cannot reach a dominant position. In the same way subadults are very
376 marginal in agonistic networks and they perform aggression towards far fewer individuals than do adults;
377 this is consistent with results for yellow-bellied marmots (Wey & Blumstein, 2010). This is probably
378 because one year old individuals have not yet reached the physical strength to compete with adults
379 (Mann, Macchi, & Janeau, 1993). We were not able to include exact age in the analysis due to lack of
380 data for many marmots first captured as adults, but we expect that in adults, older individuals would show
381 higher levels of agonism. In fact, this tendency has been demonstrated in yellow-bellied marmots (Wey,
382 & Blumstein, 2010) and other mammals (Büttner, Scheffler, Czycholl, & Krieter, 2015). Dominance
383 status frequently increases with age as competitive abilities improve (e.g. Verhulst, Geerdink, Salomons,
384 & Boonekamp, 2014), and in cooperatively breeding species, older subordinates usually take the place of
385 dominants when they die (Wiley & Rabenold, 1984).

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

402 On the other hand, received interactions do not show sex differences and this can perhaps be explained
403 because of inter-sex aggression, a behavior also found in the yellow-bellied marmot (Armitage, 1974) and
404 one that is frequently observed in our study population (we reported 37 cases out of 167 total aggressive
405 interactions in year 2018 alone). Although an explanation for this behavior in marmots was not
406 investigated here, inter-sex aggression with other group members could occur due to territoriality against

407 dispersed individuals that become part of the group, sexual aggression among mating partners (King,
408 1973), or during intense territorial fights (each of these examples were observed during data collection).
409 While females perform less aggression than males, a lack of difference in received interactions, i.e. in-
410 degree and in-strength, could be explained by a higher male-to-female aggression (for females the lower
411 rates of aggression received from other females are probably balanced by increased rates of aggression
412 received from males). Indeed, in 2018 females received 36% of total aggression from males (20/57) while
413 males received only 14% (17/123) of aggression from females.

414 The lower level of aggression that we found in groups with pups could be an effect of a higher investment
415 in parental and extra-parental care and a subsequent reduction in aggressive behaviours. However the
416 absence of pups in social groups could reveal the absence of a stable dominant pair (it could be for
417 instance the result of infanticide by competitor males, as detected by Coulon et al., 1995), thus the higher
418 level of aggressive behaviors could be explained by a higher level of competition for the dominant role.

419 Finally, the effect we reported due to study area could be explained by a couple of factors. In our site with
420 more open areas home ranges appear to be smaller, maybe because of the higher quality of vegetation
421 (Ferrari, unpublished data). Thus a higher level of competition for dominance is more likely in the open
422 site, while in the closed site the stability of the social group could be more important in defending a
423 greater home range from neighbors. Furthermore, in the open site individuals spend less time in vigilance
424 because predators can more easily be detected (Ferrari et al., 2010). Therefore time spent in social
425 interactions, even agonistic ones, could increase (Ferrari et al., 2020 in revision).

426

427

428 **5. CONCLUSIONS**

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

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

441 Further examinations of species with a social structure based on small stable family groups are needed to
442 demonstrate the reliability of hurdle GLMMs for Social Network Analysis. Our approach could be useful
443 to test additional hypotheses about factors influencing social behavior in small social groups, including

444 the effects of other individual and group level characteristics (e.g. personality) on social structure, or the
445 effects of group-level patterns of aggressive/affiliative behavior on reproductive success.

446

447

448 **REFERENCES:**

449 Akaike, H. (1974), A new look at the statistical model identification. *IEEE Transactions on Automatic*
450 *Control*, 19(6), 716-723. <https://doi.org/10.1109/TAC.1974.1100705>

451 Alexander, R. D. (1974). The Evolution of Social Behavior. *Annual Review of Ecology and Systematics*,
452 5(1), 325–383. <https://doi.org/10.1146/annurev.es.05.110174.001545>

453 Allainé, D. (2000). Sociality, mating system and reproductive skew in marmots: evidence and hypotheses.
454 *Behavioural Processes*, 51(1–3), 21–34. [https://doi.org/10.1016/S0376-6357\(00\)00116-9](https://doi.org/10.1016/S0376-6357(00)00116-9)

455 Allainé, D., & Theuriau, F. (2004). Is there an optimal number of helpers in Alpine marmot family
456 groups? *Behavioral Ecology*, 15(6), 916–924. <https://doi.org/10.1093/beheco/arh096>

457 Altmann, S. (1974). Observational study of behaviour: sampling methods. *Behaviour*, 49, 227–267.
458 <https://doi.org/10.1163/156853974X00534>

459 Ancona, S., Drummond, H., & Zaldívar-Rae, J. (2010). Male whiptail lizards adjust energetically costly
460 mate guarding to male–male competition and female reproductive value. *Animal Behaviour*, 79(1),
461 75–82. <https://doi.org/10.1016/J.ANBEHAV.2009.10.005>

462 Andino N., Reus L., Cappa F., Campos V., & Giannoni S., (2011). Social environment and agonistic
463 interactions: strategies in a small social mammal. *Ethology*, 117, 992–1002.

464 Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013).
465 Individual personalities predict social behaviour in wild networks of great tits (*Parus major*).
466 *Ecology Letters*, 16(11), 1365–1372. <https://doi.org/10.1111/ele.12181>

467 Armitage, K.B. (1974). Male behaviour and territoriality in the Yellow-bellied marmot. *Journal of*
468 *Zoology*, 172, 233–265. <https://doi.org/10.1111/j.1469-7998.1974.tb04104.x>

469 Armitage, K.B. (1991). Social and population dynamics of yellow-bellied marmots: results from long-
470 term research. *Annual Reviews of Ecology and Systematics*, 22, 379–407.
471 <https://doi.org/10.1146/annurev.es.22.110191.002115>

472 Balthazart, J., & Hendrick, J. C. (1979). Relationships between the daily variations of social behavior and
473 of plasma FSH, LH and testosterone levels in the domestic duck *Anas platyrhynchos* L. *Behavioural*
474 *Processes*, 4(2), 107–128. [https://doi.org/10.1016/0376-6357\(79\)90027-5](https://doi.org/10.1016/0376-6357(79)90027-5)

475 Barash, D. P. (1976). Social behaviour and individual differences in free-living Alpine marmots
476 (*Marmota marmota*). *Animal Behaviour*, 24(1), 27–35. [https://doi.org/10.1016/S0003-3472\(76\)80096-6](https://doi.org/10.1016/S0003-3472(76)80096-6)

478 Barash, D. P. (1989). *Marmots : social behavior and ecology*. Stanford University Press.

479 Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference A Practical Information-*
480 *Theoretic Approach*. Springer, New York

481 Barthélemy M., Barrat A., Pastor-Satorras R., & Vespignani A., (2005) Characterization and modeling of
482 weighted networks. *Physica A* 346, 34. <https://doi.org/10.1016/j.physa.2004.08.047>

483 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using
484 lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>

485 Bermond, B., Mos, J., Meelis, W., van der Poel, A. M., & Kruk, M. R. (1982). Aggression induced by
486 stimulation of the hypothalamus: Effects of androgens. *Pharmacology Biochemistry and Behavior*,
487 16(1), 41–45. [https://doi.org/10.1016/0091-3057\(82\)90010-7](https://doi.org/10.1016/0091-3057(82)90010-7)

488 Blumstein, D. T., & Armitage, K. B. (1999). Cooperative Breeding in Marmots. *Oikos*, 84(3), 369.
489 <https://doi.org/10.2307/3546418>

490 Briffa, M., & Sneddon, L. U. (2007). Physiological constraints on contest behaviour. *Functional Ecology*,
491 21(4), 627–637. <https://doi.org/10.1111/j.1365-2435.2006.01188.x>

492 Büttner, K., Scheffler, K., Czycholl, I. & Krieter, J. (2015) Social network analysis - centrality parameters
493 and individual network positions of agonistic behavior in pigs over three different age levels.
494 *SpringerPlus*, 4, 185.

495 Butts C.T. (2008). Social Network Analysis with sna. *Journal of Statistical Software*, 24(6), 1–51

496 Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, 35(5),
497 1454–1469. [https://doi.org/10.1016/S0003-3472\(87\)80018-0](https://doi.org/10.1016/S0003-3472(87)80018-0)

498 Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females
499 increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences of*
500 *the United States of America*, 106(33), 13850–13853. <https://doi.org/10.1073/pnas.0900639106>

501 Cassini, M. H., (1991). Foraging under predation risk in the wild guinea pig *Cavia aperea*. *Oikos*,
502 62, 20-24. <https://doi.org/10.2307/3545441>

503 Chase, I.D. (1982) Dynamics of Hierarchy Formation: the Sequential Development of Dominance
504 Relationships. *Behaviour*, 80, 218–239. <https://doi.org/10.1163/156853982X00364>.

505 Cohas, A., Yoccoz, N. G., & Allainé, D. (2007). Extra-pair paternity in alpine marmots, *Marmota*
506 *marmota*: genetic quality and genetic diversity effects. *Behavioral Ecology and Sociobiology*, 61(7),
507 1081–1092. <https://doi.org/10.1007/s00265-006-0341-7>

508 Cole, H. W., Parente, F. J., Peeke, H. V. S., & Figler, M. H. (1980). The Relationship Between Sex and
509 Aggression in Convict Cichlids (*Cichlasoma Nigrofasciatum* Günther). *Behaviour*, 75(1), 1–21.
510 <https://doi.org/10.1163/156853980X00537>

511 Collias, N.E. (1944) Aggressive Behavior among Vertebrate Animals. *Physiological Zoology*, 17, 83–
512 123. <https://doi.org/10.1086/physzool.17.1.30151832>.

513 Costantini, D., Carere, C., Caramaschi, D., & Koolhaas, J. M. (2008). Aggressive and non-aggressive
514 personalities differ in oxidative status in selected lines of mice (*Mus musculus*). *Biology Letters*,
515 4(1), 119–122. <https://doi.org/10.1098/rsbl.2007.0513>

516 Costantini, D., Ferrari, C., Pasquaretta, C., Cavallone, E., Carere, C., von Hardenberg, A., & Réale, D.
517 (2012). Interplay between plasma oxidative status, cortisol and coping styles in wild alpine

518 marmots, *Marmota marmota*. *The Journal of Experimental Biology*, 215 (2), 374–383

519 Coulon J., Graziani L., Allainé D., Bel M.C., Poudroux S. (1995) Infanticide in the alpine marmot
520 (*Marmota marmota*). *Ethology, Ecology and Evolution*, 7, 191-194

521 Crawley, M. J. (2007). *The R book*. England: John Wiley & Sons, Ltd.

522 Croft, D. P., James, R., & Krause (2008). *Exploring Animal Social Networks*. Princeton University Press:
523 Princeton, NJ.

524 Croft, D. P., Madden, J. R., Franks, D. W., & James, R. (2011). Hypothesis testing in animal social
525 networks. *Trends in Ecology & Evolution*, 26(10), 502–507.
526 <https://doi.org/10.1016/J.TREE.2011.05.012>

527 Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research.
528 *InterJournal Complex systems*, 1695

529 deCarvalho, T. N., Watson, P. J., & Field, S. A. (2004). Costs increase as ritualized fighting progresses
530 within and between phases in the sierra dome spider, *Neriene litigiosa*. *Animal Behaviour*, 68(3),
531 473–482. <https://doi.org/10.1016/J.ANBEHAV.2003.08.033>

532 de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of
533 dominance hierarchies. *Animal Behaviour*, 71, 585-592.
534 <https://doi.org/10.1016/j.anbehav.2005.05.015>

535 Dorning, J., Harris, S. (2019). Individual and seasonal variation in contact rate, connectivity and centrality
536 in red fox (*Vulpes vulpes*) social groups. *Scientific Reports* 9, 20095.
537 <https://doi.org/10.1038/s41598-019-56713-3>

538 Edwards, D. A. (1969). Early androgen stimulation and aggressive behavior in male and female mice.
539 *Physiology & Behavior*, 4(3), 333–338. [https://doi.org/10.1016/0031-9384\(69\)90185-1](https://doi.org/10.1016/0031-9384(69)90185-1)

540 Ebensperger, L.A. & Blumstein, D.T. (2006) Sociality in New World hystricognath rodents is linked to
541 predators and burrow digging. *Behavioral Ecology*, 17, 410–418.
542 <https://doi.org/10.1093/beheco/arj048>

543 Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network
544 analysis. *Journal of Animal Ecology*, 84(5), 1144–1163. <https://doi.org/10.1111/1365-2656.12418>.

545 Ferrari, C., Bogliani, G., & von Hardenberg, A. (2010). Alpine marmots (*Marmota marmota*) adjust
546 vigilance behaviour according to environmental characteristics of their surrounding. *Ethology
547 Ecology & Evolution*, 21, 355–364. <https://doi.org/10.1080/08927014.2009.9522490>.

548 Ferrari C., Pasquaretta C., Caprio E., Ranghetti L., Bogliani G., Rolando A., Bertolino S., Bassano B.,
549 von Hardenberg (2020). Extrinsic and intrinsic factors affecting Alpine marmots' time budget.
550 *Ethology, Ecology and Evolution*, in revision.

551 Ferrari, C., Pasquaretta, C., Carere, C., Cavallone, E., von Hardenberg, A., & Réale, D. (2013). Testing
552 for the presence of coping styles in a wild mammal. *Animal Behaviour*, 85(6), 1385–1396.
553 <https://doi.org/10.1016/J.ANBEHAV.2013.03.030>

554 Ferrari, C., Pasquaretta, C., von Hardenberg, A., & Bassano, B. (2012). Intraspecific killing and

555 cannibalism in adult Alpine marmots *Marmota marmota*. *Ethology Ecology and Evolution*, 24, 388–
556 394. <https://doi.org/10.1080/03949370.2012.683454>

557 Freeman, L. C. (1979). Centrality in social networks: conceptual clarification. *Social Networks*, 1, 215–
558 239.

559 Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L., & Sherwin, W. B. (2010). Social and
560 genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the*
561 *National Academy of Sciences of the United States of America*, 107(46), 19949–19954.
562 <https://doi.org/10.1073/pnas.1007997107>

563 Gammell, M. P., de Vries, H., Jennings, D. J., Carlin, C. M., & Hayden, T. J. (2003). David's score: a
564 more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Animal Behaviour*,
565 66(3), 601–605. <https://doi.org/10.1006/anbe.2003.2226>

566 Hack, M. A. (1997). The energetic costs of fighting in the house cricket, (*Acheta domesticus*) L.
567 *Behavioral Ecology*, 8(1), 28–36. <https://doi.org/10.1093/beheco/8.1.28>

568 Hackländer, K., Möstl, E., & Arnold, W. (2003). Reproductive suppression in female Alpine marmots,
569 *Marmota marmota*. *Animal Behaviour*, 65(6), 1133–1140. <https://doi.org/10.1006/ANBE.2003.2159>

570 Hamede, R. K., Bashford, J., McCallum, H., & Jones, M. (2009). Contact networks in a wild Tasmanian
571 devil (*Sarcophilus harrisi*) population: using social network analysis to reveal seasonal variability in
572 social behaviour and its implications for transmission of devil facial tumour disease. *Ecology*
573 *Letters*, 12(11), 1147–1157. <https://doi.org/10.1111/j.1461-0248.2009.01370.x>

574 Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*,
575 7(1), 1–16. [https://doi.org/10.1016/0022-5193\(64\)90038-4](https://doi.org/10.1016/0022-5193(64)90038-4)

576 Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*,
577 7(1), 17–52. [https://doi.org/10.1016/0022-5193\(64\)90039-6](https://doi.org/10.1016/0022-5193(64)90039-6)

578 Higham, J. P., Heistermann, M., & Maestriperi, D. (2011). The energetics of male–male endurance
579 rivalry in free-ranging rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, 81(5), 1001–1007.
580 <https://doi.org/10.1016/J.ANBEHAV.2011.02.001>

581 Huang, B., Wey, T. W., & Blumstein, D. T. (2011). Correlates and Consequences of Dominance in a
582 Social Rodent. *Ethology*, 117(7), 573–585. <https://doi.org/10.1111/j.1439-0310.2011.01909.x>

583 Jennions, M. D., & Macdonald, D. W. (1994). Cooperative breeding in mammals. *Trends in Ecology &*
584 *Evolution*, 9(3), 89–93. [https://doi.org/10.1016/0169-5347\(94\)90202-X](https://doi.org/10.1016/0169-5347(94)90202-X)

585 Johns, D. W. & Armitage, K. B. (1979). Behavioral ecology of alpine yellow-bellied marmots.
586 *Behavioral Ecology and Sociobiology*, 5, 133–157.

587 King, J. A. (1973). The ecology of aggressive behavior. *Annual Review of Ecology and Systematics*, 4,
588 117–38.

589 Krause, J., Croft, D. P., & James, R. (2007). Social network theory in the behavioural sciences: potential
590 applications. *Behavioral Ecology and Sociobiology*, 62(1), 15–27. [https://doi.org/10.1007/s00265-](https://doi.org/10.1007/s00265-007-0445-8)
591 007-0445-8

592 Krause, J., Lusseau, D., & James, R. (2009). Animal social networks: an introduction. *Behavioral*
593 *Ecology and Sociobiology*, 63(7), 967–973. <https://doi.org/10.1007/s00265-009-0747-0>

594 Low, M. (2006). The energetic cost of mate guarding is correlated with territorial intrusions in the New
595 Zealand stitchbird. *Behavioral Ecology*, 17(2), 270–276. <https://doi.org/10.1093/beheco/arj025>

596 Lüdecke D, Makowski D, Waggoner P, Patil I (2020). “performance: Assessment of Regression Models
597 Performance.” CRAN. doi: 10.5281/zenodo.3952174

598 Lukas, D., & Clutton-Brock, T. (2012). Life histories and the evolution of cooperative breeding in
599 mammals. *Proceedings of the Royal Society of London B: Biological Sciences*, 279(1744), 4065–
600 4070. <https://doi.org/10.1098/RSPB.2012.1433>

601 Madden, J. R., Drewe, J. A., Pearce, G. P., & Clutton-Brock, T. H. (2011). The social network structure
602 of a wild meerkat population: 3. Position of individuals within networks. *Behavioral Ecology and*
603 *Sociobiology*, 65(10), 1857–1871. <https://doi.org/10.1007/s00265-011-1194-2>

604 Magurran, A.E. & Garcia, C.M. (2000) Sex differences in behaviour as an indirect consequence of mating
605 system. *Journal of Fish Biology*, 57, 839–857. <https://doi.org/10.1111/j.1095-8649.2000.tb02196.x>

606 Maldonado-Chaparro, A. A., Hubbard, L., & Blumstein, D. T. (2015). Group size affects social
607 relationships in yellow-bellied marmots (*Marmota flaviventris*). *Behavioral Ecology*, 26(3), 909–
608 915. <https://doi.org/10.1093/beheco/arv034>

609 Mann, C. S., Macchi, E., & Janeau, G. (1993). Alpine marmot (*Marmota marmota*, L.). *IBEX Journal of*
610 *Mountain Ecology I*: 17-30.

611 Marchant, J. N., Mendl, M. T., Rudd, A. R., & Broom, D. M. (1995). The effect of agonistic interactions
612 on the heart rate of group-housed sows. *Applied Animal Behaviour Science*, 46(1–2), 49–56.
613 [https://doi.org/10.1016/0168-1591\(95\)00636-2](https://doi.org/10.1016/0168-1591(95)00636-2)

614 Maynard Smith, J. (1974). The theory of games and the evolution of animal conflicts. *Journal of*
615 *Theoretical Biology*, 47(1), 209–221. [https://doi.org/10.1016/0022-5193\(74\)90110-6](https://doi.org/10.1016/0022-5193(74)90110-6)

616 Maynard Smith, J., & Price, G. R. (1973). The Logic of Animal Conflict. *Nature*, 246(5427), 15–18.
617 <https://doi.org/10.1038/246015a0>

618 Michener, G. (1980). The measurement and interpretation of interaction rates: an example with adult
619 Richardson’s Ground Squirrels. *Biol. Behav.*, 5(4), 371–384.

620 Mullahy, J. (1986). Specification and testing of some modified count data models. *Journal of*
621 *Econometrics*, 33(3), 341–365. doi:10.1016/0304-4076(86)90002-3

622 Newman, M. E. J. (2003). The structure and function of complex networks. *SIAM Review. Society for*
623 *Industrial and Applied Mathematics Publications*

624 Newman, M. E. J. (2004). Analysis of weighted networks, *Physical Review*, E 70, 056131

625 Opsahl, T. (2009). Structure and Evolution of Weighted Networks. *University of London (Queen Mary*
626 *College), London, UK, 104–122.*

627 Pasquaretta, C., Bogliani, G., Ranghetti, L., Ferrari, C., & von Hardenberg, A. (2012). The Animal
628 Locator: a new method for accurate and fast collection of animal locations for visible species.

629 *Wildlife Biology*, 18(2), 202–214. <https://doi.org/10.2981/10-096>

630 Pasquaretta, C., Busia, L., Ferrari, C., Bogliani, G., Reale, D., & von Hardenberg, A. (2015). Helpers
631 influence on territory use and maintenance in Alpine marmot groups. *Behaviour*, 152(10), 1391–
632 1412. <https://doi.org/10.1163/1568539X-00003284>

633 Perrin, C., Coulon, J., and Le Berre, M. (1993). Social behavior of alpine marmots (*Marmota marmota*):
634 seasonal, group, and individual variability. *Canadian Journal of Zoology*, 71, 1945 - 1953.
635 <https://doi.org/10.1139/z93-278>

636 Pinheiro, J. C., & Bates, D. M. (1995). Approximations to the Log-Likelihood Function in the Nonlinear
637 Mixed-Effects Model. *Journal of Computational and Graphical Statistics*, 4(1), 12–35.
638 <https://doi.org/10.1080/10618600.1995.10474663>

639 Pinheiro, J. C. (2014). Linear mixed effects models for longitudinal data. *Wiley StatsRef: Statistics*
640 *Reference Online*. <https://doi.org/10.1002/9781118445112.stat05514>

641 Pinter-Wollman, N. (2015). Persistent variation in spatial behavior affects the structure and function of
642 interaction networks. *Current Zoology*, 61(1), 98–106. <https://doi.org/10.1093/czoolo/61.1.98>

643 Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S., McDonald, D.
644 B. (2013). The dynamics of animal social networks: analytical, conceptual, and theoretical
645 advances. *Behavioral Ecology*, 25(2), 242–255. <https://doi.org/10.1093/beheco/art047>

646 R core team. (2018). R: A language and environment for statistical computing. R Foundation for
647 Rammal, H., Bouayed, J., & Soulimani, R. (2010). A direct relationship between aggressive
648 behavior in the resident/intruder test and cell oxidative status in adult male mice. *European Journal*
649 *of Pharmacology*, 627(1–3), 173–176. <https://doi.org/10.1016/J.EJP.2009.11.001>

650 Rizopoulos, D. (2019). GLMMadaptive: Generalized Linear Mixed Models using Adaptive
651 Gaussian Quadrature. R package version 0.5-1. <https://cran.r-project.org/package=GLMMadaptive>

652 Rovero, F., Hughes, R. N., Whiteley, N. M., & Chelazzi, G. (2000). Estimating the energetic cost of
653 fighting in shore crabs by noninvasive monitoring of heartbeat rate. *Animal Behaviour*, 59, 705–713.
654 <https://doi.org/10.1006/anbe.1999.1353>

655 Schülke O., Bhagavatula J., Vigilant L., & Ostner J., (2010) Social bonds enhance reproductive success in
656 male macaques. *Current Biology*, 20, 2207–2210. <https://doi.org/10.1016/j.cub.2010.10.058>

657 Shen, S.-F., Akçay, E., & Rubenstein, D. R. (2014). Group Size and Social Conflict in Complex
658 Societies. *The American Naturalist*, 183(2), 301–310. <https://doi.org/10.1086/674378>

659 Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: new insights and issues for
660 behavioral ecologists. *Behavioral Ecology and Sociobiology*, 63(7), 975–988.
661 <https://doi.org/10.1007/s00265-009-0725-6>

662 Silk, J. B. (2007). Social components of fitness in primate groups. *Science*, 317, 1347.
663 <https://doi.org/10.1126/science.1140734>

664 Silk M.J., Jackson A.L., Croft D.P., Colhoun K., & Bearhop S. (2015) The consequences of
665 unidentifiable individuals for the analysis of an animal social network. *Animal Behavior*, 104, 1–11.

666 doi:10.1016/j.anbehav.2015.03.005

667 Simon, N. G., Whalen, R. E., & Tate, M. P. (1985). Induction of male-typical aggression by androgens
668 but not by estrogens in adult female mice. *Hormones and Behavior*, 19(2), 204–212.
669 [https://doi.org/10.1016/0018-506X\(85\)90019-4](https://doi.org/10.1016/0018-506X(85)90019-4)

670 Sosa, S. (2016). The Influence of Gender, Age, Matriline and Hierarchical Rank on Individual Social
671 Position, Role and Interactional Patterns in *Macaca sylvanus* at ‘La Forêt des Singes’: A Multilevel
672 Social Network Approach. *Frontiers in Psychology*, 7, 529.
673 <https://doi.org/10.3389/fpsyg.2016.00529>

674 Sosa, S., Sueur, C. & Puga-Gonzalez, I. (2020). Network measures in animal social network analysis:
675 their strengths, limits, interpretations and uses. *Methods in Ecology and Evolution*.
676 <https://doi.org/10.1111/2041-210x.13366>

677 Stine, R. A. (1995). Graphical Interpretation of Variance Inflation Factors. *The American Statistician*,
678 49(1), 53–56. doi:10.1080/00031305.1995.10476113

679 Swenson, R. O. (1997). Sex-role reversal in the tidewater goby, *Eucyclogobius newberryi*. *Environmental*
680 *Biology of Fishes*, 50(1), 27–40. <https://doi.org/10.1023/A:1007352704614>

681 Tu, W. (2006). Zero-Inflated Data. *Encyclopedia of Environmetrics* doi:10.1002/9780470057339.vaz000

682 Türk, A., & Arnold, W. (1988). Thermoregulation as a limit to habitat use in alpine marmots (*Marmota*
683 *marmota*). *Oecologia*, 76(4), 544–548. <https://doi.org/10.1007/BF00397867>

684 Turner, J. W., Bills, P. S., & Holekamp, K. E. (2018). Ontogenetic change in determinants of social
685 network position in the spotted hyena. *Behavioral Ecology and Sociobiology*, 72(1), 10.
686 <https://doi.org/10.1007/s00265-017-2426-x>

687 Van De Pol, M., & Wright, J. (2008). A simple method for distinguishing within- versus between-subject
688 effects using mixed models, *Animal behavior*, 77, 753-758.
689 <https://doi.org/10.1016/j.anbehav.2008.11.006>

690 Verhulst, S., Geerdink, M., Salomons, H.M. & Boonekamp, J.J. (2014) Social life histories: jackdaw
691 dominance increases with age, terminally declines and shortens lifespan. *Proceedings of the Royal*
692 *Society B: Biological Sciences*, 281, 20141045. <https://doi.org/10.1098/rspb.2014.1045>

693 Wasserman, S., & Faust, K. (1994). *Social Networks Analysis: Methods and Applications*. Cambridge
694 *University Press, Cambridge, UK*.

695 Webber, Q.M.R. & Vander Wal, E. (2019) Trends and perspectives on the use of animal social
696 network analysis in behavioural ecology: a bibliometric approach. *Animal Behaviour*,
697 149, 77-87. <https://doi.org/10.1016/j.anbehav.2019.01.010>

698 Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a
699 promising tool for the study of sociality. *Animal Behaviour*, 75(2), 333–344.
700 <https://doi.org/10.1016/J.ANBEHAV.2007.06.020>

701 Wey, T. W., & Blumstein, D. T. (2010). Social cohesion in yellow-bellied marmots is established through
702 age and kin structuring. *Animal Behaviour*, 79(6), 1343–1352.

703 <https://doi.org/10.1016/J.ANBEHAV.2010.03.008>

704 Wey, T. W., & Blumstein, D. T. (2012). Social attributes and associated performance measures in
705 marmots: bigger male bullies and weakly affiliating females have higher annual reproductive
706 success. *Behavioral Ecology and Sociobiology*, 66(7), 1075–1085.
707 <https://doi.org/10.1007/s00265-012-1358-8>

708 Whitehead, H. (2008). *Analyzing animal societies : quantitative methods for vertebrate social analysis*.
709 University of Chicago Press.

710 Wiley, R.H. & Rabenold, K.N. (1984) The evolution of cooperative breeding by delayed reciprocity and
711 queuing for favourable social positions. *Evolution*, 38, 609–621. <https://doi.org/10.2307/2408710>

712 Zelenka, G. (1965). Observations sur l'écologie de la marmotte des alpes. *Tierre Vie*, 19, 238–256

713 Zomeño, C., Birolo, M., Zuffellato, A., Xiccato, G. & Trocino, A. (2017) Aggressiveness in group-
714 housed rabbit does: Influence of group size and pen characteristics. *Applied Animal Behaviour*
715 *Science*, 194, 79–85. <https://doi.org/10.1016/j.applanim.2017.05.016>