



HAL
open science

Reliable hypotheses testing in animal social network analyses: global index, index of interactions and residual regression

Sebastian Sosa, Cristian Pasquaretta, Ivan Puga-Gonzalez, F Stephen Dobson, Vincent A Viblanc, William Hoppitt

► To cite this version:

Sebastian Sosa, Cristian Pasquaretta, Ivan Puga-Gonzalez, F Stephen Dobson, Vincent A Viblanc, et al.. Reliable hypotheses testing in animal social network analyses: global index, index of interactions and residual regression. 2022. hal-03862221

HAL Id: hal-03862221

<https://hal.science/hal-03862221v1>

Preprint submitted on 21 Nov 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Reliable hypotheses testing in animal social network analyses: global 2 index, index of interactions and residual regression

3 Sebastian Sosa¹, Cristian Pasquaretta², Ivan Puga-Gonzalez³, F Stephen Dobson^{1,4}, Vincent A
4 Viblanc¹, William Hoppitt⁵

5
6 ¹ Université de Strasbourg, CNRS, IPHC, UMR 7178, Strasbourg, France

7 ² Research Center on Animal Cognition, Center for Integrative Biology, National Center for Scientific
8 Research (CNRS), University of Toulouse (UPS), Toulouse, France

9 ³ Institute for Global Development and Planning, University of Agder, Kristiansand, Norway

10 ⁴ Department of Biological Sciences, Auburn University, Auburn, AL, USA

11 ⁵ School of Biological Sciences, Royal Holloway, University of London, Egham, UK

12

13

14 **Abstract**

15 Animal social network analyses (ASNA) have led to a foundational shift in our understanding
16 of animal sociality that transcends the disciplinary boundaries of genetics, spatial movements,
17 epidemiology, information transmission, evolution, species assemblages and conservation.
18 However, some analytical protocols (i.e., permutation tests) used in ASNA have recently been
19 called into question due to the unacceptable rates of false negatives (type I error) and false
20 positives (type II error) they generate in statistical hypothesis testing. Here, we show that
21 these rates are related to the way in which observation heterogeneity is accounted for in
22 association indices. To solve this issue, we propose a method termed the “global index” (GI)
23 that consists of computing the average of individual associations indices per unit of time. In
24 addition, we developed an “index of interactions” (II) that allows the use of the GI approach
25 for directed behaviours. Our simulations show that GI: 1) returns more reasonable rates of
26 false negatives and positives, with or without observational biases in the collected data, 2) can
27 be applied to both directed and undirected behaviours, 3) can be applied to focal sampling,
28 scan sampling or “gambit of the group” data collection protocols, and 4) can be applied to
29 first- and second-order social network measures. Finally, we provide a method to control for
30 non-social biological confounding factors using linear regression residuals. By providing a
31 reliable approach for a wide range of scenarios, we propose a novel methodology in ASNA
32 with the aim of better understanding social interactions from a mechanistic, ecological and
33 evolutionary perspective.

34 INTRODUCTION

35 Over the past 50 years, graph theory has established itself as an important methodology in the
36 study of natural or artificial interconnected systems (anthropology¹, sociology², economics³,
37 ecology⁴, ethology⁵, animals societies⁶) whether at a microscopic (e.g., proteomic⁷) or
38 macroscopic (e.g., ecosystem⁸) scale. In regards to the study of animal sociality, novel
39 methods (i.e., indices of associations and pre-network permutations) building upon traditional
40 graph theory have allowed to address issues specific to this field (e.g., heterogeneity in
41 sampling effort). Hence, animal social network analysis (ASNA) has become an important
42 methodology for major advances in both theoretical and empirical research on animal
43 sociality^{4,9}, social ontogeny¹⁰, genetic mechanisms of sociality¹¹, impact on fitness¹²,
44 epidemiology¹⁰, animal culture¹⁰, and social structures (e.g., social structure diversity and
45 evolution¹³⁻¹⁶). These achievements were made possible thanks to the establishment of
46 analytical methods that were considered state-of-the-art protocols.

47 ASNA typically has two key-objectives: 1) estimating sociality patterns among individuals,
48 quantified in a social network and 2) testing statistical hypotheses regarding patterns of
49 sociality among individuals (as described further). To accomplish the first objective,
50 researchers calculate a measure of the tendency to associate (i.e., undirected behaviour) or
51 interact (i.e., directed behaviour)¹⁷⁻¹⁹ (i.e., social index) for each pair of individuals (dyad).
52 The resulting set of values is used to construct a social network, with each individual as a
53 node and the values of the social index providing an index of the strength of the connection
54 (edge weight) between members of each dyad. To account for individual heterogeneity in
55 sociality and observation frequency, Hubalek¹⁷, Sailer¹⁸ and Whitehead¹⁹ provided a
56 theoretical background to measure social affiliations with association indices. This has
57 become a fundamental building block for describing social structures in ecological research.
58 Many of the association indices that exist⁶ estimate the proportion of time that a pair of
59 individuals spends in association. The higher the value of the index, the greater the level of
60 association within the dyad. The most frequently used association index to date is the simple
61 ratio index -SRI- (*Eqn. 1*), designed for data that were collected in discrete sampling periods.

$$SRI = \frac{x_{ab}}{y_a + y_b + y_{ab} + x_{ab}} \quad (\text{Eqn. 1})$$

62 x_{ab} is the number of sampling periods with a and b observed associated, y_a is the number of
63 sampling periods with only a identified, y_b is the number of sampling periods with only b
64 identified and y_{ab} is the number of sampling periods with a and b identified but not
65 associated.

66

67 However, association indices only provide a measure of associations between individuals, but
68 do not inform on the direction of social interactions. In contrast, interaction networks are
69 often constructed when a particular type of interaction is the focus. In contrast to associations,
70 interactions are usually directional (e.g., preening in birds), and can differ from association
71 networks because the directionality of interactions is considered (e.g., bird *A* preens bird *B*
72 frequently, but bird *B* does not preen bird *A*) seldomly. In this paper, we focus initially on
73 association networks, but discuss how the methods can be extended to interaction networks in
74 the second part of the paper.

75 To accomplish the second objective (testing statistical hypotheses about sociality), node-based
76 measures are often used. Node-based measures are calculated from the network and they
77 measure aspects of each individual's position in the network²⁰ (e.g., individual frequencies of
78 associations/interactions: *strength*). Hypotheses testing typically relates to node-based
79 measures, such as whether males have a higher *strength* than females. However, node-based
80 measures cannot be used in a straightforward manner to test hypotheses about individual
81 associations, because associations (as well as social interactions) are statistically dependent:
82 they are counted twice, once for each individual of the dyad. This dependence violates
83 parametric test assumptions by artificially inflating the degrees of freedom. Because degrees
84 of freedom represent the number of values in the final calculation of a statistic that are free to
85 vary, their inflation can generate high rates of false positives²¹. In addition, associations may
86 be influenced by sampling biases and non-social factors²². The consequence may be a biased
87 conclusion about the significance of the individuals' associations, when one focuses on
88 traditional testing against a null hypothesis (H_0). Consequently, much of the methodological
89 work in ASNA has focused on developing techniques that enable valid hypotheses testing.
90 Such techniques are needed to provide a low rate of false negatives, that is the non-rejection
91 of a false hypothesis (e.g., a conclusion that males and females on average have similar
92 *betweenness*, when in fact males have higher *betweenness*). At the same time, one must avoid
93 the risk of inflating false positives, that is the rejection of the null hypothesis when it is true
94 (e.g., a conclusion that males have a higher *strength* than females, when in fact there is little
95 difference between the sexes). More specifically, we would want to reject a null hypothesis
96 that is true at the 5% significance level only 5% of the time: any more than this is an inflation
97 of the false positive error rate. The use of parametric statistics in social network analyses

98 typically results in inflated error rates due to the problem of non-independence in the data
99 described above.

100 One way to achieve valid hypothesis testing in ASNA is to resort to the use of permutation
101 techniques²³. Permutation methods consist first in computing a test statistic on real data (e.g.,
102 a *t* statistic for the difference in *strength* between males and females), then randomizing the
103 original dataset a certain number of times (e.g., 10,000 times) while keeping any pattern that
104 may have existed in the real data (e.g., males no longer have a higher *strength*), and finally the
105 test statistic is recalculated from the permuted data to yield a null distribution for the test
106 statistic, which is used in place of a parametric null distribution (e.g., a *t* distribution in our
107 example) - this statistic is taken to be a representative value if the null hypothesis were
108 correct-. In ASNA, permutation²³ techniques can take two forms, network or pre-network
109 permutations. A variety of network permutation approaches exist (see Hobson, et al.²⁴ for a
110 review) and the most frequently used is the node label permutation approach that consists of
111 randomizing individuals' characteristics rather than aspects of their sociality. Instead of
112 randomizing individuals' characteristics, pre-network permutations (also called data stream
113 permutations)²³ are performed on the raw data, after each permutation the network is
114 reconstructed and a new test statistic is generated for the null distribution. The manner of
115 randomization must be carefully chosen, so that it disrupts the pattern being tested for (e.g.,
116 males having higher *strength* than females), but also maintains any statistical dependencies in
117 the data that might cause a false positive. Consequently, pre-network permutations usually
118 consist of generating a randomized alternative dataset constrained by the biological features
119 of the original dataset by maintaining 1) the same total number of individuals, 2) the same
120 number of dyads observed, 3) the same number of times each individual is observed and 4)
121 the same number of individuals in each group. It must be noted, though, that pre-network
122 permutations have been used primarily for the study of associations and not for the study of
123 interactions. This is perhaps because interactions are often directed in nature, e.g., bird *A*
124 attacks bird *B*, or chimpanzee *C* grooms chimpanzee *D*, and the definition of association-
125 based indices like the SRI (eq.1) only allow for undirected relationships. For the study of
126 individual interactions, researchers have mainly applied network permutations that were
127 directly performed on networks that were calculated using indices designed specifically for
128 interaction data and allow the study of directed social behaviors (e.g., allogrooming,
129 aggression) (see Croft, et al.¹² for further details). Nonetheless, the combination of indices of

130 associations with both pre-network permutations and network permutations have become
131 standard testing protocols in ASNA, but have recently been called into question^{25,26}.

132 Recent studies have identified important reliability issues related to the pre- and network
133 permutation analytical protocols, such as inflated rates of false negatives (i.e., non-rejection of
134 a false null hypothesis) and false positives (i.e., acceptance of a false null hypothesis) for both
135 permutation approaches^{25,26}. For example, Puga-Gonzalez, et al.²⁵ used simulations for a case
136 with data biases arising from the data collection protocol (e.g., oversampling of specific
137 individual categories), and found that pre-network permutations showed rates of false
138 positives of 35.6%, while network permutations showed rates of false negatives of 60.8% and
139 rates of false positives of 36.6%. Yet, very few biological data collected *in natura* are immune
140 to biases related to the system under study or related to necessarily limited sampling. Given
141 the central role of pre-network and network permutations in ASNA, high rates of false
142 negatives and false positives are likely to be a common problem and a pressing issue to
143 resolve for ensuring the reliability of hypotheses testing in ASNA.

144 Whereas important statistical advances have helped improve the reliability of statistical
145 hypothesis testing^{20,22} in ANSA, limitations remain. Franks, et al.²⁰ proposed the use of linear
146 regression for testing, while adding control factor(s) to account for potential biases. However,
147 this approach was only validated for undirected association data using pre-network
148 permutations and inclusion of additional variables in the model reduce degree of freedom.
149 Farine & Carter 2021²² suggested an approach using both permutation processes to estimate
150 the deviance from randomness, but this approach still returns high rates of false positives and
151 can only be used for association data. Finally, Hart, et al.²⁷ recently demonstrated that
152 parametric tests without permutations show rates of false positives and false negatives similar
153 to those of network permutation tests, thereby calling into question the use of permutations
154 themselves. Moreover, although authors argue that permutations do not control for data
155 dependency, the purpose of permutations is to provide an alternative to compute a test statistic
156 against null models and to avoid reducing the degree of freedom of parametric tests. As a
157 result, it currently remains difficult to identify a standard analytical protocol in ASNA,
158 according to the type of data collected and the data collection protocol.

159 Here, we propose an approach for addressing the issue of high rates of false positives and
160 false negatives. The main idea behind our approach is that indices of associations measure the
161 proportion of time that a dyad spends in association, however, while the computation of these
162 indices considers the sampling effort, indices of associations are calculated using absolute

163 time (i.e., a SRI of 0.5 means that a dyad spends 50% of the time associated, regardless of
164 whether individuals were observed 10 times or 100 times). Thus, in order to account for
165 sampling effects, indices of associations need to be weighted to obtain a value relative to the
166 sampling effort. We term this the “global index” (GI) approach. In addition, as indices of
167 associations have been designed only for undirected behaviours, we also developed an “index
168 of interactions” (II) that estimates the proportion of interactions of a dyad, while accounting
169 for both received and given behaviours and allowing the use of GI for directed behaviours.

170 Sampling biases are only one aspect of the problem and, as described by Farine & Carter
171 2021²², these factors can be of two different types. First, indices of associations may be
172 altered by sampling biases (i.e., observation time heterogeneity) related to the data collection
173 protocol or to individuals’ specificities (e.g., cryptic individuals are more challenging to
174 observe). The second potential confounding factor that may influence individual associations
175 refers to non-social biological influences of sociality such as cycle synchrony across
176 individuals, space use or kinship, among others. The consideration of potential confounding
177 non-social biological influences on sociality is of major interest in order to correctly evaluate
178 the effect of sociality. While Farine & Carter 2021²² proposed some solutions to control for
179 such confounding factors, these show the same limitations previously discussed (high rates of
180 false positives and applicable only to association data). Moreover, developing a methodology
181 allowing to reach beyond the control for putative biological confounding factors, by assessing
182 their magnitude or importance on social interactions, remains to be done. In the third part of
183 our study, we propose a method to control for non-social biological confounding influences
184 (e.g., sex, age, body condition). Our approach uses linear regressions to estimate the
185 relationship between an assumed non-social biological confounding factor and a social
186 measure. If the relationship is significant, we can then consider that the non-social biological
187 confounding factor affects the individual social measure. We can “control” for the factor by
188 computing the residuals from the linear regression and using them as a relative social
189 measure. This approach, defined as the “residual correction” (RC), has the advantage of being
190 usable after accounting for sampling biases (after using GI), using permutation approaches to
191 compute significant relationships, estimating whether one or several non-social biological
192 confounding factor(s) exist, and statistically controlling for these factors. Furthermore, the use
193 of generalized linear mixed models allows accounting for structure of the data (e.g., repeated
194 measurements and non-Gaussian distributions like Poisson, or zero-inflated distributions).

195 Finally, it is possible to test for non-linear relationships between the social measure and the
196 potential non-social biological confounding factor(s) through polynomial regressions.

197 We perform computer simulations and first demonstrate that the GI approach (that consists in
198 considering individuals' sampling effort within the indices of associations) is reliable for the
199 study of undirected behaviors. In a second step, we show that the index of interactions (II) can
200 be reliably used in combination with the GI to study directed behaviours. Finally, we show
201 that the RC approach accurately estimates and controls for non-social biological confounding
202 factors. Our simulations mimic a number of different sampling (focal sampling or scan
203 sampling or "gambit of the group" -described below-) and recording protocols²⁹ (continuous
204 and timed sampling) commonly used to collect ASNA data, highlighting that our methods
205 generate reliable results, there are observation biases, variations in the data collection
206 protocol, or the type of behaviour studied (directed/interactions or undirected/associations).

207

208 **METHOD & RESULTS**

209 *Issue related to control of observations - time heterogeneity*

210 While indices of associations accurately estimate differences in associations among the
211 individuals from different dyads, numerous confounding factors may affect these associations.
212 Several studies have attempted to control for such confounding factors. For example, as
213 highly gregarious individuals associate more frequently with other highly gregarious
214 conspecifics just by chance, even if there is no mutual affiliation, Godde et al.³⁰ suggested
215 consideration of the individuals of a dyad. Similarly, in order to account for the specificities in
216 gregariousness between categories of individuals, Peeper et al.³¹ suggested some
217 modifications to the computation of association indices. The Peeper et al. 1999 and Godde et
218 al. 2013 approaches are conceptually similar and modify the indices of associations as
219 follows:

$$SIG_{ab} = SI_{ab} \frac{\sum SI}{\sum SI_a \sum SI_b} \text{ (Eqn. 2)}$$

220

221 where SI_{ab} is the social index for the dyad ab , $\sum SI$ is the sum of all the SIs for all dyads, and
222 $\sum SI_a$ and $\sum SI_b$ are the sums of all the SIs for individuals a and b . Note that the authors used
223 a specific social index (the half weight index- a modification of the SRI), but the logic can be
224 applied to any appropriate social index of association that measures the proportion of time
225 spent associating. The logic is that if patterns of association were governed only by each

226 individual's levels of gregariousness, we would expect the proportion of time a and b spend in
227 association to be proportional to $\sum SI_a \sum SI_b$. This would represent the case where individuals
228 associate with others at random. Consequently, dividing by $\sum SI_a \sum SI_b$ "corrects" the social
229 index, SIG_{ab} , such that it quantifies the tendency of a and b to associate after accounting for
230 their individual gregariousness. As $\sum SI$ is a constant for all dyads, it can be removed so we
231 obtain:

$$SIG_{ab} = \frac{SI_{ab}}{\sum SI_a \sum SI_b} \text{ (Eqn. 3)}$$

232 where the denominator controls for gregariousness of each individual of the dyad.
233 Here we propose a similar method (global index: GI, Eqn. 4) to control for differences in
234 sampling time among individuals, by replacing $\sum SI_a \sum SI_b$ with the sampling time of each
235 individual of the dyad. This will weight each proportion of time that two individuals spend
236 together by the inverse of each individual's total time of observation:

$$GI_{ab} = \frac{SI}{\sum S_a \sum S_b} \text{ (Eqn. 4)}$$

237 where $\sum S_a$ is the sampling effort of individual a and $\sum S_b$ is the sampling effort of individual
238 b . Note that this formula can be only used with weighted social network measures and not
239 with binary social network measures, such as the *degree* (i.e., number of social partners), that
240 only consider the presence/absence of links without considering their weights. Therefore, for
241 binary social network measures, we propose division of the social network measure by the
242 sum of the sampling efforts of the individuals for whom the social network measure is
243 computed and those of its social partners. Once the GI is used to construct the social network,
244 the same index can be used as part of a pre-network permutation process in order to test
245 hypotheses about the network. We hypothesize that this correction will solve many of the
246 problems with sampling biases described above, and test our hypothesis below using
247 computer simulations.

248

249 Concretely, if we consider discrete time sampling rule²⁹ (instantaneous or one-zero sampling)
250 such as spatial associations collected with "gambit of the group" sampling protocol (i.e.
251 considering spatially clustered individuals associated), or behavioral events without duration
252 collected with scan sampling protocol, sampling effort of an individual a would simply be the
253 number of sampling periods in which it was observed. Similarly, if we consider continuous
254 recording sampling rule of behavioral state with (e.g. time of grooming) or without (e.g.
255 frequencies of grooming) duration collected with focal sampling protocol²⁹, the sampling

256 effort of an individual a would be the time of all focal bouts made on a . The two following
257 simulations mimic both cases of behavioural recording: continuous behavioural frequencies
258 collected through focal sampling and discrete behavioural sampling (e.g., spatial associations
259 collected through GoG) to highlight how the GI performed under these sampling and
260 recording rules for undirected behaviours using the simple ratio index (i.e., $GI_{ab} = \frac{SRI_{ab}}{\sum S I_a \sum S I_b}$).

261

262 *Simulations to validate the GI method for undirected behaviours*

263 To demonstrate the reliability of the Global Index (GI) approach in multiple scenarios, we
264 used the simulation from Puga-Gonzalez et al.¹⁴. This simulation, inspired by Farine²³,
265 simulates datasets collected by focal sampling in which individuals of opposite sexes show
266 differences in sociality, whether statistically significant or not. In addition, it is possible to
267 mimic a specific amount of sampling protocol bias by simulating oversampling for males.
268 With such a simulated dataset, it is possible to test for differences in sociality between sexes
269 through network permutations, pre-network permutations, and parametric tests. Hence, this
270 simulation allows the assessment of rates of false negative error, while simulating a
271 significant difference in sociality between males and females with or without the presence of
272 sampling biases. On the other hand, when simulating similar sociality levels in males and
273 females with or without the presence of sampling bias, it is possible to assess rates of false
274 positive error. As in the simulations of Puga-Gonzalez et al. 2020²⁵, we used Latin hypercube
275 sampling³² with the ‘lhs’ R library³³ to sample the parameter space (variables a–d in Table 1).
276 500 different combinations of input parameter values were run per simulation scenario,
277 producing a total of 2,000 simulations.

278 In addition, we made two modifications to the original simulation. The first consisted of using
279 the GI approach. To compute the GI (see *Eqn.4*), we computed first the *SRI* (see *Eqn.1*). The
280 second was to compute individuals’ *degree* and *eigenvector* to validate our method also with
281 measures that consider individuals’ direct links only (first-order measures: *degree* and
282 *strength*) and a measure that considers individuals’ indirect links (second-order measure:
283 *eigenvector*)²⁰ with the R package ANTs³⁴. These changes were the only ones we made
284 regarding the evaluation of GI reliability for focal sampling (simulation 1, [Appendix 1](#)).
285 However, in order to evaluate the GI reliability for GoG, we made another modification by
286 considering each observation as a cluster of associated individuals and not a focal observation
287 (simulation 2, [Appendix 2](#)).

288 Results for simulation 1 (focal sampling) showed important improvement for network
289 permutations using the GI approach for focal sampling with rates of false negatives below 5%
290 with or without the presence of observation biases and rates of false positives below 5% with
291 observation biases and below 10% without observation biases for all social network measures
292 (Table 2). As expected, parametric tests showed high rates of false positives related to over-
293 inflation of the degree of freedom used to calculate the significance³⁵. Finally, the GI
294 approach did not solve the issue related to pre-network permutations (i.e., it did not address
295 the null hypothesis that X was distributed randomly with respect to Y or that the effect of X on
296 Y was zero) and thus, as expected, the GI did not solve the issue of high rates of false
297 positives using the pre-network approach.

298 Results for simulation 2 (scan sampling/GoG) showed similar values for reliability (Table 3)
299 with rates of false positives below 5% with or without the presence of observation biases for
300 all social network measures. Finally, whereas rates of false negatives were under 5% with
301 observation biases for all social network measures, these rates reached 93.4% in simulation
302 without biases and for the *degree* measure. This issue derives from the fact that most of
303 simulations generated fully-connected networks in which all individuals had an equal number
304 of partners (equal to the defined group size) and without biases of observation. While we
305 could have modified the simulation algorithm to avoid the creation of fully-connected
306 networks, scan/GoG sampling protocols often generate dense networks and, therefore, we
307 chose to keep the simulations as such as a warning regarding the use of binary network
308 measures under scan/GoG sampling protocol.

Table 1. Range of variation of initial parameters for simulations 1, 2 and 3

Parameter	Variable type	Range
Group sampling	Discrete	[30-100]
Female sex ratio	Continuous	[0.2-0.8]
Females' observation bias*	Continuous	[0.5-1.0]
Number of focal samples**	Discrete	[100-2000]

*In simulations without observation biases, this variable was kept constant at 1.

** In simulations with Gambit of the Group, this variable represents the number of observations

Table 2. Results for simulation 1. Overview of global index (GI) percentage of false positive/negatives for undirected behaviours with focal sampling data collection protocol according to scenarios with and without observation bias and different hypothesis testing approaches.

	Simulation with biases of observation						Simulation without biases of observation					
	False negative rates (%)			False positive rates (%)			False negative rates (%)			False positive rates (%)		
	Degree	Strength	Eigenvector	Degree	Strength	Eigenvector	Degree	Strength	Eigenvector	Degree	Strength	Eigenvector
<i>Parametric test</i>	5	2.6	0.6	6.6	40.2	30	2.4	0.4	0	3.2	3.6	3.6
<i>Network permutation test</i>	4.6	1	0.4	3.4	0.6	0.2	0	0.4	0	3.6	3.4	4
<i>Pre-network permutation test</i>	65.8	16.4	28.4	38	13.2	23	42.2	65.8	59.2	60	15.2	14.2

Table 3. Results for simulation 2. Overview of global index (GI) percentage of false positive/negatives for undirected behaviours with GoG data collection protocol according to scenarios with and without observation bias and different hypothesis testing approaches.

	Simulation with biases of observation						Simulation without biases of observation					
	False negative rates (%)			False positive rates (%)			False negative rates (%)			False positive rates (%)		
	Degree	Strength	Eigenvector	Degree	Strength	Eigenvector	Degree	Strength	Eigenvector	Degree	Strength	Eigenvector
<i>Parametric test</i>	1.2	0	0	98.6	14.4	13	97	0	0	5.6	6.8	6.8
<i>Network permutation test</i>	1	0	0	98.8	2	2.4	96.8	0	0	4.8	5.2	5.2
<i>Pre-network permutation test</i>	100	100	100	0	0	0	100	100	100	0	0	0

Extension of GI approach to directed behaviours

While individuals' associations are mostly used in behavioral ecology in which entire populations are followed over large areas, the study of individuals' social interactions are also an important part of ASNA research. The study of social interactions is usually done in smaller and well-identified groups. In order to enable reliable testing for questions about social interactions, we developed an index of interactions (II) and evaluated the reliability of the combination of II with GI through a third simulation.

The appropriate form of an index of social interactions (the II approach) for directed behaviours depends on the recording rule used to collect data, which depends in part on the nature of the target interaction. Here we showed that for interaction data collected in discrete sampling periods (instantaneous or one-zero sampling), a modified version of the SRI is appropriate, but that if the interaction data were collected using continuous recording, then a simple ratio is more appropriate.

The first possibility is that the target interaction is a behavioural state of a meaningful duration, e.g., bouts of grooming. The researcher might then wish to estimate the proportion of time that each dyad (ab , consisting of individuals a and b) spends engaged in the target interaction. Under such cases, instantaneous sampling may be used²⁹, with the data specifying whether the target interaction was occurring for each dyad at uniform time points (e.g., every 5 mins). In this case the II approach is directly analogous to the collection of standard association data, therefore the SRI (Eqn. 1) can be used except, x_{ab} is the number of sampling points at which a and b were observed interacting with one another, y_a is the number of sampling points at which only a was identified, y_b is the number of sampling points at which only b was identified and y_{ab} is the number of sampling points at which a and b were identified but not engaged together in the target interaction. Again y_{null} , here the number of points at which neither a nor b were identified, was not included in the calculation. In simple terms, the II approach calculated the proportion of points at which a and b were observed interacting, but excluded the cases where the researcher is not sure if they were interacting or not.

It is also straightforward to extend the II approach to directed interactions, e.g. if we want to separately estimate the proportion of time a spends grooming b , and the proportion of time b spends grooming a .

$$II_{a \rightarrow b} = \frac{x_{a \rightarrow b}}{(y_a + y_b) + y_{ab} + x_{a \rightarrow b} + x_{b \rightarrow a}} \quad (\text{Eqn. 5})$$

Here $x_{a \rightarrow b}$ is the number of sampling points at which a was directing an interaction towards b (e.g., a was grooming b) and $x_{b \rightarrow a}$ is the number of sampling points at which b was directing an interaction towards a (e.g., a was grooming b). Therefore, for such data the SRI, or the II approach (Eqn. 2), can be used under the same assumptions as for association data: e.g., failing to observe individuals a and b while they are interacting is as likely as failing to observe them both when they are not interacting together (see Hoppitt & Farine 2018).

Alternatively, the target interaction may be a behavioural event of short duration (e.g., one bird directs a peck at another bird), or the researcher may simply be interested in the rate at which a initiated interactions with b , rather than the proportion of time engaged in that interaction. In such cases one-zero sampling is traditionally used²⁹. Here the data specify whether or not at least one event $a \rightarrow b$ occurred in each sampling period of length X . Here we could intuitively use the II approach given in Eqn. 5, with suitably modified definitions of the terms: e.g., $x_{a \rightarrow b}$ is now the number of sampling periods during which a was observed directing an interaction towards b , y_a is the number of sampling periods for which only a was identified and y_{ab} is the number of sampling periods for which a and b were identified but not engaged together in the target interaction. Here the directed $II_{a \rightarrow b}$ estimates the probability of seeing at least one interaction directed from a to b in a time period of length X , again under equivalent assumptions as the SRI for association data³⁶. The researcher may prefer to convert this to an estimate of the rate at which interactions $a \rightarrow b$ occur as $\lambda_{a \rightarrow b} = -\log(1 - II_{a \rightarrow b})/X$.

Simulation on directed behaviours: Focal sampling and continuous recording

In order to simulate datasets of directed interactions collected through focal sampling with continuous recording (simulation 3, [Appendix 3](#)), we modified simulation 1 by assigning directionality to what was originally considered associations. For simplicity, we considered all observations as emitted behaviours. For each simulated dataset, we computed the GI (see *Eqn.4*) using the II (see *Eqn.5*) as social index. This allowed us to assess the reliability of the II and GI, with or without sampling biases and with or without relationship between emitted behaviours and individuals' sex. We ran node label permutations and parametric tests using the Latin hypercube sampling with the 'lhs' R library³³ to sample input parameter space (Table 1). For each scenario, we ran 500 different combinations of input parameter values for a total of 2,000 simulations. In this simulation, as well as in the following one, we did not perform pre-network permutations for two reasons. First, because data stream permutations for

directed behaviours do not exist, and second because the GI approach does not solve pre-network permutation reliability issues related to hypothesis testing, as discussed earlier.

Results of simulation showed that the combination of II and GI returns low rates of false positives and false negatives, with or without sampling biases for node label permutations and parametric test (Table 3). The low rates of false positives and false negatives of parametric tests in these simulations for directed behaviours are supported by the fact that, as these data are independent (an emitted interaction is counted once), over-inflation of the degree of freedom should not occur even when testing hypothesis in scenarios with observational biases. This is why, in such scenarios, parametric tests should be preferred. However, it is quite common that researchers use several directed social network measures (total emitted behaviours and total received behaviours) in a linear regression to evaluate their effect. In such cases, data independence is violated as an individual's emitted behaviours are the received behaviours of its congeners and thus a single behaviour is counted twice. In this scenario, network permutations should be preferred.

Table 4. Results for simulation 3. Overview of global index (GI) percentage of false positive/negatives for directed behaviours with focal sampling data collection protocol according to scenarios with and without observation bias and different hypothesis testing approaches.

	Simulation with biases of observation						Simulation without biases of observation					
	False negative rates (%)			False positive rates (%)			False negative rates (%)			False positive rates (%)		
	Outdegree	Outstrength	Outeigenvector	Outdegree	Outstrength	Outeigenvector	Outdegree	Outstrength	Outeigenvector	Outdegree	Outstrength	Outeigenvector
<i>Parametric test</i>	2.2	5.4	0.2	4.6	6.2	6.8	1.4	6.2	0.4	6.2	4.2	6
<i>Network permutation test</i>	1.6	3.4	0	4.2	4.8	6.6	1.6	5.4	0.2	6.8	4.6	7.8

Simulation on directed behaviours: Scan sampling and discrete time sampling

In order to simulate datasets of directed interactions collected through discrete time sampling, we created a simulation that mimics scan sampling (simulation 4, [Appendix 4](#)). This model creates a population of size N with a predefined number of subgroups (g , 4 subgroups in each simulation) within the population. By creating subgroups, we created *cliques* with groups of individuals having higher probability of being observed together, yet seldomly interacting, thereby shaping the y_{ab} term of the Π in Eqn.5. A number of scans (x) was predefined at initialization of the simulation. For each observation, a within and between subgroups interaction process was defined. In the within subgroup interaction process, a subgroup (g) was selected randomly, a number of individuals (n) observed within the scan (i) was defined following a Poisson distribution (with alpha of 6). Once the size of the scan was defined, $n/2$ individuals belonging to the subgroup g were selected, and these individuals (defined as *emitters*) will emit an interaction based on a fixed probability (P_1) towards a selected subgroup member. In this way, and according to the probability P_1 , we can create a network with a given amount of preferential attachment (i.e. individuals interact preferentially or not with the same individuals). In the case where an *emitter* did not have social partners, an interaction toward a social partner belonging to subgroup (g) was randomly created. In the between groups interaction process, a fixed probability (P_2) was defined to enable within the scan (i) the presence of individual(s) that do not belong to the selected subgroup g . For each of these individuals, an incoming link from an individual belonging to the selected subgroup g was created. This interaction processes (within and among subgroups) were iteratively repeated until the defined set of observations (x) reached a desired value. The simulation input parameters (N , x , P_1 , P_2) are listed in Table 5.

Once the simulation was done, we calculated the GI (see Eqn.4) using the Π (see Eqn.5) as social index and the directed versions of the previous social measures were computed for each individual through Π and GI: 1) *outstrength*, *outdgree* and *outeigenvector*. To assess the reliability of hypothesis testing, a random continuous variable (x) following a normal distribution was created. This variable, that represents an individual trait, was then ordered and assigned based on individuals' social measures, to create a relationship between x and social measures (scenario 1), and also randomly assigned to individuals' strength to create no relationship between x and social measures (scenario 2).

In order to mimic observational biases (z) proportional to the relationship between the variable x and the social measures, a maximum observational bias was defined (e.g. 20%) as

input parameter of the simulations (Table 5), and this percentage decreased proportionally to the relative position of the individual according to its value x . For example, the individual showing the highest x had its number of observations reduced by 20%. The second individual (the one with the second highest x) had its number of observations reduced by $\frac{20}{2}\%$, the third individual by $\frac{20}{3}\%$, and so on. This allowed us to create scenarios with or without biases in combination with scenarios 1 and 2 explained above.

To evaluate the testing reliability of II combined with the GI approach, we performed 500 simulations for scenario 1 and 500 simulations for scenario 2. This was done with and without observational biases for a total of 2,000 simulations. We sampled the input parameter space of the simulations (variables a–e in Table 5) using the Latin hypercube sampling using ‘lhs’ R library. For each simulation, we assessed the rates of false negatives and false positives of network permutations and parametric tests.

Results of simulation showed that the combination of II and GI returned low rates of false positives and false negatives, with or without sampling biases for node label permutations and parametric test (Table 6). When observation biases were simulated, we observed that parametric test still returned no false positive nor false negative results, whereas we started to observe some false negative and false positive results with network permutations, although the rates still fell within acceptable levels (Table 6).

Table 5. Range of variation of initial parameters for simulation 4

Parameter	Variable type	Range
a) Population size (N)	Continuous	30-100
b) Probability to interact with former social partners ($P1$)	Continuous	0.1-0.3
c) Probability of presence of individual(s) that do not belong to the sampled subgroup ($P2$)	Continuous	0.4-0.7
d) Set of observations to reach (x)	Continuous	0.2-0.80
e) Observational biases (z)	Continuous	1-20

Table 6. Results for simulation 4. Overview of global index (GI) percentage of false positive/negatives for directed behaviours with scan sampling data collection protocol according to scenarios with and without observation biases and different hypothesis testing approaches.

	Simulation with biases of observation						Simulation without biases of observation					
	False negative rates (%)			False positive rates (%)			False negative rates (%)			False positive rates (%)		
	Outdeg ree	Outstren gth	Outeigenvec tor	Outdeg ree	Outstren gth	Outeigenvec tor	Outde gree	Outstre ngth	Outeigenve ctor	Outde gree	Outstreng th	Outeigenvect or
<i>Parametric test</i>	0.6	0	8.4	2	0	1.8	3.6	0	0.2	2.6	0	2.2
<i>Network permutation test</i>	0.4	3	8.4	2	0.6	1.8	3.6	0	0.2	2.4	0.2	2.2

Estimating and controlling for non-social biological confounding factors

Finally, to be able to estimate and control for non-social biological confounding factors, we used residuals of the regression between the social measure and the potential non-social biological confounding factors. As residuals represent the difference between the prediction of the linear regression model of the relationship between the predictive variable (the potential non-social biological confounding factor(s)) and the predicted variable (the social measure), they allowed us to adjust the social measure according to the potential non-social biological confounding factor(s), and use it as relative social measure. As discussed in the introduction, the residual correction (RC) method has the advantage of being usable after accounting for sampling biases (after using GI), of using permutation approaches to compute significant relationships, and of estimating whether one or several non-social biological confounding factor(s) exist. Furthermore, it is possible to resort to generalized linear mixed models in order to account for structure of the data (e.g., repeated measurements, non-Gaussian distribution such as Poisson, or zero-inflated distributions). Finally, non-linear relationships can be tested between the social measure and the potential non-social biological confounding factor(s) with the use of polynomial regressions.

To assess the reliability of RC, we used the Farine & Carter 2021²² simulation (simulation 5, [Appendix 5](#)) that mimics association data collected on a population using GoG sampling and a discrete time recording rule. Each individual had a trait value T_i drawn from a normal distribution. By assigning individuals with the highest trait values to the largest observed groups X (ranging from 1 to 10) or by assigning individuals to observed groups randomly, the simulation created, respectively, scenarios where individuals' traits impacted their spatial associations or scenarios where individuals' traits had no impact on their spatial associations. In addition, a conceptual modification to the simulation was done to mimic the effect of a non-social biological confounding factor. This modification consisted of considering individuals' group size X as the result of spatial preference, where individuals in large groups live on large patches that contain more resources and therefore have a greater carrying capacity. With this modification, individuals' spatial associations were no longer considered as a result of individual social decisions only, but rather as an outcome of habitat heterogeneity and individual space use. This is an ideal simulation to evaluate the reliability of the RC approach as in such scenario the social measure is related to individuals' traits but individuals' sociality is an indirect outcome of individuals' spatial preferences. In addition, Farine & Carter 2021²² simulation showed that standard permutation tests (pre-network and

network permutations) return high rates of false positives while this should not occur because this social measure is an outcome of habitat heterogeneity and individual space use as discussed previously.

We ran 39,600 of the modified simulations sampling the parameter space with 100 simulations for each possible combination of population size (ranging from 30 to 150) and number of observations per individuals (ranging from 30 to 60). For each simulated dataset, we computed the *strength*, *eigenvector* and *degree* and performed analyses with and without the RC approach for node label permutations. We expect to observe no significant relationship between individuals' traits and spatial associations when using RC, whereas a significant relationship should be found without RC (as highlighted by simulations in Farine & Carter 2021²²). Thus, the RC approach accurately estimates and controls for non-social biological confounding factors for both first- and second-order network measures. As in simulation 1, rates of false positives and false negatives with or without observation biases for the *degree* were very high for the same reasons as explained in simulation 1 (i.e., GoG simulation creates highly connected networks). Finally, when the RC approach was not used, the rates of false positives increased drastically, indicating that it is important to control for non-social biological confounding factors in order to obtain reliable statistical results.

Table 7. Range of variation of initial parameters for simulation 5

Parameter	Variable type	Range
Population size	Continuous	30-150
Number of observations	Continuous	30-60

Table 8. Results for simulation 5. Overview of regression correction (RC) combined with global index (GI) percentage of false positives for undirected behaviours with GoG data collection protocol according to scenarios with non-social biological confounding factors.

	Without RC (%)			With RC (%)		
	Degree	Strength	Eigenvector	Degree	Strength	Eigenvector
<i>Parametric test</i>	84.06	99.9	100	5.6	0.15	3.06
<i>Network permutation test</i>	87.52	100	100	5.53	0.59	8.16

DISCUSSION

In the present study, we developed a Global Index (GI), an approach that weights dyadic association/interaction indices according to their respective sampling effort. Simulations show that this method returns acceptable rates of false negatives and false positives errors, with or without biases of observations. The GI approach can be used for both directed and undirected behaviours using focal sampling, scan sampling or Gambit of the Group data collection protocols, and can be used for first-order (*degree* and *strength*) and second-order (*eigenvector*) social network measures. Our simulations show that pre-network permutations as well as parametric tests for ASNA return unacceptable rates of false negatives and false positives, even using the GI approach, and suggest these should be avoided for ASNA research to ensure reliable hypothesis testing. Finally, we also provide a method to estimate and control for non-social biological confounding factors using the residuals of individuals' social measure values regressed on the estimate of confounding factors, showing reliable results. One major asset of this approach is that it can be combined with the GI to account for multiple confounding factors at once and takes into account the data structure (e.g., repeated measurements, spatial or phylogenetical observation clustering, non-Gaussian distribution). However, while the original simulations from Ivan et al. 2020 and Farine & Carter 2021 simulated datasets with some sample sizes lower than 30, we modified the minimum sample size ($N \geq 30$) for all simulations, as these use parametric tests (linear regressions) to test statistical hypotheses. Further tests might determine whether GI and II, in combination with non-parametric tests, provide reliable statistical results.

Together with the growing interest and use of graph theory for research on social complexity, variance analysis (e.g., intraclass correlation coefficient for the study of repeatability) is starting to be used in ASNA³⁷ and, to date, hypothesis testing reliability for those approaches have not been tested and should thus be considered cautiously. Similarly, temporal analyses of individuals' sociality is an important part of ASNA to understand sociality dynamics arising from demographic^{38,39} variation, environment⁴⁰, and ontogeny⁴¹. However, as for variance analyses, those require further testing of the reliability of the mixed models that are used to study them. Nonetheless, our results show that high rates of false negatives and false positives are not related to the permutations themselves but rather to an issue with control of observation time heterogeneity. We expect that “node label” permutations with GI approach we propose here is also reliable for variance analysis or other more complex hypothesis testing approaches, although further tests are needed. By providing a reliable approach for a

wide range of scenarios, we propose a novel methodology in ASNA with the aim of better understanding animal sociality and animals' societies from a mechanistic, ecological and evolutionary perspective.

ACKNOWLEDGMENT

This research was supported by fellowship grant from the Institute of Advanced Studies of the University of Strasbourg to F.S.D. and V.A.V. F.S.D. thanks the Région Grand Est and the Eurométropole de Strasbourg for the award of a Gutenberg Excellence Chair. We also thank Benjamin Beltzung for the discussions regarding index of sociality issues.

REFERENCES

- 1 Apicella, C. L., Marlowe, F. W., Fowler, J. H. & Christakis, N. A. Social networks and cooperation in hunter-gatherers. *Nature* **481**, 497-501 (2012).
- 2 Milgram, S. The small world problem. *Psychology Today* **2**, 60-67 (1967).
- 3 Ter Wal, A. L. & Boschma, R. A. Applying social network analysis in economic geography: framing some key analytic issues. *The Annals of Regional Science* **43**, 739-756 (2009).
- 4 Sosa, S., Jacoby, D. M., Lihoreau, M. & Sueur, C. (2021).
- 5 Sueur, C., Jacobs, A., Amblard, F., Petit, O. & King, A. J. How can social network analysis improve the study of primate behavior? *American Journal of Primatology* **73**, 703-719 (2011).
- 6 Whitehead, H. *Analyzing animal societies: quantitative methods for vertebrate social analysis*. (University of Chicago Press, 2008).
- 7 Ravasz, E., Somera, A. L., Mongru, D. A., Oltvai, Z. N. & Barabási, A.-L. Hierarchical organization of modularity in metabolic networks. *science* **297**, 1551-1555 (2002).
- 8 Ulanowicz, R. E., Holt, R. D. & Barfield, M. Limits on ecosystem trophic complexity: insights from ecological network analysis. *Ecology letters* **17**, 127-136 (2014).
- 9 Puga-Gonzalez, I., Sosa, S. & Sueur, C. Social networks analyses in primates, a multilevel perspective. *Primates* **60**, 163-165 (2019).
- 10 Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, A. M. & Fischer, J. Motivational shifts in aging monkeys and the origins of social selectivity. *Current Biology* **26**, 1744-1749 (2016).
- 11 Brent, L. J. *et al.* Genetic origins of social networks in rhesus macaques. *Scientific Reports* **3**, 1042 (2013).
- 12 Ilany, A., Holekamp, K. E. & Akçay, E. Rank-dependent social inheritance determines social network structure in spotted hyenas. *Science* **373**, 348-352 (2021).
- 13 Papageorgiou, D. & Farine, D. R. Multilevel societies in birds. *Trends in ecology & evolution* **36**, 15-17 (2021).
- 14 Sueur, C., Romano, V., Sosa, S. & Puga-Gonzalez, I. Mechanisms of network evolution: a focus on socioecological factors, intermediary mechanisms, and selection pressures. *Primates* **60**, 167-181 (2019).
- 15 Balasubramaniam, K. N. *et al.* The influence of phylogeny, social style, and sociodemographic factors on macaque social network structure. *American Journal of Primatology* (2017).
- 16 Sosa, S. Structural Architecture of the Social Network of a Non-Human Primate (*Macaca sylvanus*): A Study of Its Topology in La Forêt des Singes, Rocamadour. *Folia Primatologica* **85**, 154-163 (2014).

- 17 Hubalek, Z. Coefficients of association and similarity, based on binary (presence-absence)
data: an evaluation. *Biological Reviews* **57**, 669-689 (1982).
- 18 Sailer, L. D. & Gaulin, S. J. Proximity, sociality, and observation: the definition of social
groups. *American Anthropologist*, 91-98 (1984).
- 19 Whitehead, H. Testing association patterns of social animals. *Animal Behaviour* **57**, F26-F29
(1999).
- 20 Sosa, S., Sueur, C. & Puga-Gonzalez, I. Network measures in animal social network analysis:
Their strengths, limits, interpretations and uses. *Methods in Ecology and Evolution* **n/a**,
doi:10.1111/2041-210x.13366.
- 21 MacKinnon, D. P. & Fairchild, A. J. Current directions in mediation analysis. *Current
directions in psychological science* **18**, 16-20 (2009).
- 22 Farine, D. R. & Carter, G. G. Permutation tests for hypothesis testing with animal social
network data: Problems and potential solutions. *Methods in Ecology and Evolution* **00**, 1-13,
doi:<https://doi.org/10.1111/2041-210X.13741> (2021).
- 23 Bejder, L., Fletcher, D. & Bräger, S. A method for testing association patterns of social
animals. *Animal behaviour* **56**, 719-725 (1998).
- 24 Hobson, E. A. *et al.* A guide to choosing and implementing reference models for social
network analysis. *arXiv preprint arXiv:2012.04720* (2020).
- 25 Puga-Gonzalez, I., Sueur, C. & Sosa, S. Null models for animal social network analysis and
data collected via focal sampling: Pre-network or node network permutation? *Methods in
Ecology and Evolution* **n/a**, doi:10.1111/2041-210x.13400.
- 26 Weiss, M. N. *et al.* Common datastream permutations of animal social network data are not
appropriate for hypothesis testing using regression models. *bioRxiv* (2020).
- 27 Hart, J. D., Weiss, M. N., Brent, L. J. & Franks, D. W. Common Permutation Methods in
Animal Social Network Analysis Do Not Control for Non-independence. *bioRxiv* (2021).
- 28 Farine, D. R. & Carter, G. G. Permutation tests for hypothesis testing with animal social data:
problems and potential solutions. *BioRxiv* (2020).
- 29 Bateson, M. & Martin, P. *Measuring behaviour: an introductory guide*. (Cambridge
University Press, 2021).
- 30 Godde, S., Humbert, L., Côté, S. D., Réale, D. & Whitehead, H. Correcting for the impact of
gregariousness in social network analyses. *Animal Behaviour* **85**, 553-558 (2013).
- 31 Pepper, J. W., Mitani, J. C. & Watts, D. P. General gregariousness and specific social
preferences among wild chimpanzees. *International Journal of Primatology* **20**, 613-632
(1999).
- 32 Stein, M. Large sample properties of simulations using Latin hypercube sampling.
Technometrics **29**, 143-151 (1987).
- 33 Carnell, R. (2018).
- 34 Sosa, S. *et al.* A multilevel statistical toolkit to study animal social networks: the Animal
Network Toolkit Software (ANTs) R package. *Scientific Reports* **10**, 1-8 (2020).
- 35 Farine, D. R. & Whitehead, H. Constructing, conducting and interpreting animal social
network analysis. *Journal of Animal Ecology* **84**, 1144-1163 (2015).
- 36 Hoppitt, W. J. & Farine, D. R. Association indices for quantifying social relationships: how to
deal with missing observations of individuals or groups. *Animal Behaviour* **136**, 227-238
(2018).
- 37 Albery, G. F. *et al.* Multiple spatial behaviours govern social network positions in a wild
ungulate. *Ecology Letters* **24**, 676-686 (2021).
- 38 Borgeaud, C., Sosa, S., Sueur, C. & Bshary, R. The influence of demographic variation on
social network stability in wild vervet monkeys. *Animal Behaviour* **134**, 155-165 (2017).
- 39 Borgeaud, C., Sosa, S., Bshary, R., Sueur, C. & Van de Waal, E. Intergroup variation of social
relationships in wild vervet monkeys: a dynamic network approach. *Frontiers in psychology* **7**
(2016).
- 40 Burns, D. D., Franks, D. W., Parr, C. & Robinson, E. J. Ant colony nest networks adapt to
resource disruption. *Journal of Animal Ecology* (2020).

- 41 Sosa, S. The influence of gender, age, matriline and hierarchical rank on individual social position, role and interactional patterns in *Macaca sylvanus* at 'La Forêt des singes': A multilevel social network approach. *Frontiers in psychology* **7** (2016).