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1 *Research Article*

2 **The frequency and position of stable associations offset** 3 **their transitivity in a diversity of vertebrate social networks**

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7

8 **Abstract:** When the estimated strength of social associations corresponds to the proportion of time spent together, strong
9 links, those that take up most of the recorded time of individuals, are compulsorily transitive and tend to occur in clusters.
10 However, I describe three ways in which the frequency and position of strong associations apparently offset the expected
11 transitivity of strong links in published association networks from 26 species of vertebrates. Instead of occurring in groups
12 of three, strong links were mostly isolated. When they did occur in clusters, the clusters were small. The phenomena in-
13 creased in intensity as the overall number of links of all strengths and the overall network transitivity increased. Since
14 stable transitive motifs are beneficial to cooperation, these results can help explain why cooperative behaviors are not more
15 frequent than they are in group-living vertebrates. Inversely, stable transitive motifs may be rare and small because the
16 benefits of cooperation do not overcome the costs associated with these motifs. The summary statistics developed for this
17 study captured information not conveyed by other network-level metrics; thus they may help quantify the socio-spatial
18 structure of populations and potentially tease apart the environmental, species-specific, and individual drivers.

19 **Keywords:** clustering coefficient; graph theory; intransitivity; socio-spatial structure; peer of a peer; epidemiology; strength
20 of weak ties

21 **Significance statement:**

- 22 • Stable transitive motifs are rare and small in 26 species of group-living vertebrates.
- 23 • The article describes new network-level statistics of the frequency of strong links, the dissimilarity of link
24 strengths within triangles, and the relative fragmentation of the subnetwork of strong links.
- 25 • Results help explain why cooperation is not more frequent in group-living vertebrates
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29 Introduction

30 Granovetter (1973) observed that strong friendships between humans tend to be transitive. In other
31 words, when individual A has two best friends B and C, then B and C are also usually best friends. The
32 proximate reasons for this transitivity include the “theory of cognitive balance” stating that good friends want
33 their feelings towards third parties to be congruent (Heider, 1958), and “network homophily”, meaning that
34 strong friendships tend to emerge from (and to further promote) similarity in cultural tastes etc. (McPherson et
35 al., 2001). As a result, the networks feature clusters or cliques of individuals that are tightly-knit together.
36 There are still weak ties between these cliques, which do not obey the same transitivity rules. These weak ties
37 then perform a major role as the connections between, and the gateways into, the cliques: this is the “strength
38 of weak ties paradigm” (Granovetter, 1973).

39 In animal studies, strong ties are also expected to be more transitive than weak ties, but firstly because of
40 the way social ties are measured as the proportion of time that dyads spend together (Holekamp et al., 2012;
41 Rubenstein et al., 2015). Indeed, if individual A spends most of its time with B and with C, then B and C also
42 spend most of their time together. In other words, strong associations cannot be intransitive and should thus
43 be more transitive on average than weak associations. The resulting stable clusters of closely-knit individuals
44 promote the evolution of cooperative behaviors and represent a fitness advantage when cooperation is effec-
45 tive (Grinnell et al., 1995; Nowak, 2006; Silk et al., 2009; Teunissen et al., 2021). However, there are also costs to
46 life in a tight group. Costs include the rapid spread of pathogens (Morrison et al., 2021), reproductive conflicts
47 and other types of conflicts within the cliques (Datta, 1988; Holekamp et al., 2012), and impaired access to
48 information during the periods when the weak links are not active (Artime et al., 2017). If these costs exceeded
49 the benefits, the transitivity of strong links would operate as a constraint rather than an advantage.

50 The objective of the present paper is to apply several network statistics to decipher whether the transitivity
51 of strong links is offset by the way strong links are distributed in animal association networks. For this
52 purpose, I assembled a set of published animal association networks from 26 species (see methods). First, I
53 verified that strong links were indeed more transitive than weak links. Second, I quantified three aspects of the
54 distribution of link strength in the networks.

- 55 (i) The network-level Gini coefficient of inequalities (Gini, 1936) (method section 1.5). This metric is
56 an indicator of the overall rarity of strong links, i.e., the occurrence of a few very strong links
57 amidst mostly weak links. For example, a group where mother-offspring bonds are much
58 stronger than other types of associations would exhibit a high Gini coefficient if the offspring
59 were few. The alternatives are that strong links are not very different from weak links, or that
60 most of the links are strong.
- 61 (ii) The triadic dissimilarity between the three links in each triangle (a new metric, see method section
62 1.6). This metric indicates whether strong links more often occur in groups of three, or in an iso-

lated fashion. For example, if breeding pairs travel together and they both avoid other pairs and evict single individuals from foraging spots (Black & Owen, 1989), strong links (breeding pairs) would be mostly isolated, leading to an excess of weak triplets closed by a single strong link (Péron, 2022).

- (iii) The fragmentation of the subnetworks of strong links (method section 1.7). This metric indicates whether, when strong links are not isolated, the clusters of strong links are relatively small or large. For example, if there is a core group of closely tied individuals amidst a cloud of individuals that spend most of their time alone, the subnetwork of strong links should appear less fragmented than the network as a whole. By contrast, if the network is made of family units in which recent offspring are more tightly linked to their mother than older offspring, then the subnetwork of strong links, made exclusively of the links between recent offspring and their mothers, would appear more fragmented than the network as a whole.

If strong links were rare (high Gini coefficient), isolated (high triadic dissimilarity), and if any cluster of strong links was small (high fragmentation of the subnetwork of strong links), then I concluded that the expected transitivity of strong links was in effect counter-balanced by the distribution of strong links in the network. In addition, I tested whether these patterns occurred more often or more intensely in networks that have many links and many transitive motifs compared to networks that have few links and few transitive motifs. If that was the case, this would suggest a functional response, i.e., a change in the probability to create specific patterns in the social network with a change in the availability of social partners. For example, the number of social partners could influence the perceived benefits obtained from stable partners, reinforce or weaken the effect of existing relationships on the probability to create new relationships, or the attraction exerted on bonded pairs by other bonded pairs. In practice, I first verified the expected transitivity of strong links. Next, I developed and applied the aforementioned three network-level statistics and correlated them to the edge density.

1. Material and methods

1.1. Definitions

Association networks (sometimes termed contact networks) refer to undirected social networks where connections occur through proximity between individuals. This definition excludes directed networks, such as dominance relationships, grooming, etc. The links (or ties, or edges) can be weighted by the relative dyadic association frequency (Holekamp et al., 2012; Rubenstein et al., 2015), hereafter termed the *link strength*.

Following previous authors (Sah et al., 2019), I considered three types of associations in this study: (i) *physical contact* or staying any amount of time within touching distance of associates, (ii) *close proximity*, a category in which I pooled nearest neighbor data and data documenting the time spent within a given radius of

96 associates (with cutoff distance and duration defined by the original authors of the source studies), and (iii)
 97 *shared group membership*, which mostly applies in a fission-fusion context.

98 *Triplets* correspond to situations where one individual A is associated with two different individuals B
 99 and C. In a *transitive* association network, most triplets are closed by a link between B and C, thereby forming a
 100 *triangle* (Granovetter, 1973; Newman et al., 2002). The unweighted *transitivity score* of an association network,
 101 hereafter denoted \mathcal{C}_0 , corresponds to the proportion of closed triangles among all the triplets (Newman et al.,
 102 2002). Several adjacent triangles make a *transitive motif* or a transitive cluster or a clique. Examples of com-
 103 pletely intransitive networks include grid-like and tree-like networks (Newman, 2008). Some researchers use
 104 the clustering coefficient instead of the transitivity score which differ from the transitivity score because the
 105 clustering coefficient averages an individual transitivity score whereas the transitivity score averages a triplet
 106 score (Barrat et al., 2004). Importantly, the interpretation of the transitivity score depends on whether the links
 107 are undirected, as is the case in this study, or directed. In dominance networks, the links are directed, and the
 108 transitivity score measures the linearity of the social hierarchy (McDonald & Shizuka, 2013). In association
 109 networks which are the topic of the present study, the links are not directed, and the transitivity score
 110 measures the frequency and size of transitive motifs.

111 The triplets can be also weighed according to the strength of the links inside of them, in order to generate
 112 a *weighted transitivity score* (Opsahl & Panzarasa, 2009), hereafter denoted \mathcal{C}_1 . If \mathcal{C}_1 is larger than \mathcal{C}_0 , the
 113 probability that a triplet is closed increases with the strength of the links inside of it, and inversely if \mathcal{C}_1 is
 114 smaller than \mathcal{C}_0 then weak triplets are on average more likely to be closed than strong triplets (Opsahl &
 115 Panzarasa, 2009).

116 Another approach to the quantification of transitive clusters is to consider them as modules of individuals
 117 that interact more among themselves than with the rest of the network. Strong links would then correspond to
 118 within-module links and weak links would correspond to cross-module links. The network *modularity* quanti-
 119 fies how distinct these modules are, i.e., how rare and weak are the links between modules (Newman et al.,
 120 2002; Pons & Latapy, 2005). In practice, I delineated the modules using the short random walk communi-
 121 ty-finding algorithm (routine `cluster_walktrap` from `igraph`; Pons & Latapy, 2005). Except when ex-
 122 plicitly stated otherwise, I took into account the weight of the links when delineating the modules (argument
 123 `weights = E(graph)$weight`). I then computed the modularity score following the usual formula
 124 (Newman, 2008).

125 Lastly the *edge density*, denoted \mathcal{D}_0 , corresponds to the overall number of links in the network divided by
 126 the maximum possible number of links if all individuals were connected to each other. The edge density
 127 measures the overall probability that a link exists between any two individuals.

128 1.2. Literature search for network association data

129 This study uses published data only. Original data were collected in accordance with relevant institu-
 130 tional and national guidelines, as explained in the source articles listed in Table 1.

131 I focused on vertebrates that always or mostly forage in groups and/or always or mostly roost in groups,
 132 but without any criteria regarding the occurrence of cooperative behaviors within those groups. The data
 133 needed to be collected from free-ranging groups with naturally occurring kinship structure, and to document
 134 one of the aforementioned association types (see section 1.1). I first searched open data repositories: dryad.com
 135 and <https://bansallab.github.io/asnr/about.html> (“A social network repository” or ASNR; Sah et al., 2019) on
 136 Jan 5, 2022. Next, I used the search engine googlescholar.com with the keywords “animal” and “social net-
 137 work”. I searched the citation network of the first 60 hits upward and downward. The cutoff number 60 was
 138 chosen as a tradeoff between the risk of missing a poorly-cited study and the risk of oversight due to the sheer
 139 task at hand. If the title or abstract indicated that data corresponding to the above criterion existed, I elicited
 140 data sharing over email. This procedure yielded data from 26 species and three taxonomic classes.

141 These original studies varied in the way they quantified dyadic association rates. The most frequent
 142 method was to use the co-occurrence frequency relative to each associate’s own frequency in the dataset. Sev-
 143 eral studies however reported indexes derived from activity time budget analyses, and a few reported a dis-
 144 cretized index of association strength. To standardize the link strengths across datasets, I rescaled the link
 145 strengths between 0 and 1 using a logit-transformation so that the median point between the weakest and
 146 strongest links of each network was attributed strength 0.5.

147 The seasonal timing of data collection was decided by the original authors. I did not select data according
 148 to that criterion.

149 1.3. *Verifying the natural transitivity of strong links*

150 I used two tests of the natural transitivity of strong links. First, I compared the unweighted transitivity
 151 score \mathcal{C}_0 and the weighted transitivity score \mathcal{C}_1 (Opsahl & Panzarasa, 2009). If strong links are more transi-
 152 tive than weak links, then triplets made of strong links are more likely to be closed than triplets made of weak
 153 links, and thus I expect $\mathcal{C}_1 > \mathcal{C}_0$.

154 Second, I manipulated the networks by removing an increasing proportion of the weakest links. I com-
 155 puted the quantity $b(Q) = \frac{\mathcal{C}_0(Q) - \mathcal{D}_0(Q)}{1 - \mathcal{D}_0(Q)}$ where Q is the proportion of remaining links and \mathcal{D}_0 is the edge den-
 156 sity. If $\mathcal{D}_0(Q) = 1$, then also $\mathcal{C}_0(Q) = 1$ and $b(Q) = 1$. Note that this is the only section where \mathcal{C}_0 and \mathcal{D}_0
 157 depend on Q . In the rest of the paper, I report the values corresponding to $Q = 100\%$, i.e., unmanipulated
 158 networks, meaning that $\mathcal{D}_0 = \mathcal{D}_0(100\%)$ and $\mathcal{C}_0 = \mathcal{C}_0(100\%)$.

159 The quantity $b(Q)$ takes value 0 under the null hypothesis that the manipulated network is not more
 160 transitive than expected from the overall probability of a link occurring anywhere in the manipulated net-
 161 work. Otherwise, $b(Q)$ varies between $-\frac{\mathcal{D}_0(Q)}{1 - \mathcal{D}_0(Q)}$ for a completely intransitive network and +1 as the upper

162 boundary value for completely transitive networks. I expected b to increase as Q decreased, i.e., as I removed
 163 links. I regressed the logit-transformed b against logit-transformed Q in interaction with the initial edge den-
 164 sity, using a nonparametric spline model (function `gam` in R-package `mgcv`).

165 1.4. *Cross-species regressions*

166 In sections 1.5 to 1.7 below, I perform regressions between population-specific metrics. A potential source
 167 of spurious inference in such regressions is phylogenetic inertia, i.e., when the dependent variable is con-
 168 served along the phylogeny, and thereby pairs of closely related taxa essentially duplicate one another. If not
 169 corrected for, this mechanism can lead to over-estimate the effect sizes or the statistical significance of the
 170 results. Phylogenetic generalized models, which force the residuals of related species to be more similar than
 171 those of non related species, have become the default method to address the issue (Paradis et al., 2004). How-
 172 ever, this statistical method requests adequate sample sizes to perform, and is only necessary if there is indeed
 173 a problematic phylogenetic structure in the data. The present study has 26 species for 23 genera, and only 2.4
 174 species per taxonomic order on average (median: 1). In that situation, deep phylogenetic divergences expect-
 175 edly take precedence. The potential bias can be either major if e.g., all mammals or all primates exhibited the
 176 same values, or undetectable if e.g., the variance between the 8 primates was larger than the variance across
 177 taxonomic orders. Given these constraints and predictions, and given that preliminary analyses indicated that
 178 the second scenario was most likely (Table 1), I replaced the correlated error structure by a simple random
 179 effect of the taxonomic order. Results were qualitatively similar if removing that effect altogether.

180 1.5. *The rarity of strong links*

181 I computed the network-level Gini coefficient of inequalities between link strengths as
 182 $G = \frac{1}{2n^2\bar{x}} \sum_{i=1}^n \sum_{j=1}^n |x_j - x_i|$ where the x_i are the link strengths and n is the total number of links. The null hy-
 183 pothesis that strong links are not rare was represented by the uniform distribution of link strength, which
 184 corresponds to $G = 0.33$. If a few strong links were much stronger than the bulk of the links, G would tend
 185 towards 1. If all links were of equal strength, $G = 0$. I tested the prediction that strong links should be rarer in
 186 dense and transitive networks using a linear model with the logit-transformed Gini index as dependent vari-
 187 able and the logit-transformed edge density of the networks as predictor.

188 1.6. *Dissimilarity between the three links in each triadic relationship*

189 The objective here is to compare the three link strengths in each triad. Hereafter, a triad is any three indi-
 190 viduals with at least one non-zero link between two of the three individuals. Triads therefore include closed
 191 triangles, open triplets, but also “false triplets” corresponding to a dyad plus a disconnected individual.

192 The coefficient of variation is inadequate for this purpose because it captures the average pairwise dif-
 193 ference, and not the variability between the pairwise differences. Many different combinations of three link
 194 strengths can yield the same coefficient of variation. Therefore I derived new triad-level dissimilarity scores.
 195 For each triad, I denoted a , b , and c the three link strengths in increasing order. They varied between 0 (no

196 link) and 1 (maximum recorded strength). I measured the dissimilarity between them with ω the rescaled
 197 sum of proportional pairwise differences, and g the triad-level Gini coefficient (Péron, 2022):

$$\text{Eq. 1a} \quad \omega = \frac{a-c}{a} + \frac{b-c}{a} - 1 = \frac{b-2c}{a}$$

$$\text{Eq. 1b} \quad g = \frac{1}{2} \frac{(a-b) + (b-c) + (a-c)}{a+b+c} = \frac{a-c}{a+b+c}$$

198 These formulae reduces the 3D space $\{a, b, c\}$ into a 2D space $\{\omega, g\}$. For ease of interpretation, I suggest
 199 to divide the $\{\omega, g\}$ space into four quadrants corresponding to different triad configurations (explained in
 200 Figure 3).

201 Next, I computed graph-level triadic dissimilarity scores based on ω and g . They are simply the average
 202 of ω and g over all the triads in the network, yielding the new network-level statistics \mathcal{C}_ω and \mathcal{C}_g .

$$\text{Eq. 2a} \quad \mathcal{C}_\omega = \frac{1}{\tilde{\mathcal{J}}} \sum_{t=1}^{\tilde{\mathcal{J}}} \omega_t$$

$$\text{Eq. 2b} \quad \mathcal{C}_g = \frac{1}{\tilde{\mathcal{J}}} \sum_{t=1}^{\tilde{\mathcal{J}}} g_t$$

203 The index t refers to the triad number ($\tilde{\mathcal{J}}$ triads in total). Eqs. 2a-2b are superficially similar to the
 204 weighed transitivity score (Opsahl & Panzarasa, 2009). However I replaced the triplet strength by the triplet
 205 dissimilarity scores. The code to compute \mathcal{C}_ω and \mathcal{C}_g from the adjacency matrix is provided (Appendix S1).

206 I then devised some permutation procedures to assess whether the observed dissimilarities exceeded the
 207 expectation at random (code in Appendix S1). *Test A*: I generated full random networks by drawing 10 groups
 208 with individual probability of occurrence proportional to their frequency in the original data and computing
 209 the link strength as the co-occurrence frequency in the 10 groups. Thus, the expected association strength
 210 between two individuals A and B was the frequency of A times the frequency of B. *Test B*: To represent the
 211 edge density of the original network, I removed some links at random. To do that, I drew an Erdős–Rényi
 212 graph with the same edge density as the original network. I then assigned link strengths line by line in the
 213 adjacency matrix, by drawing them from the observed link strengths departing from the focal individual. I
 214 then rescaled the link strengths so that the sum of the link strengths in each line was proportional to the ob-
 215 servation frequency of the focal individual in the original dataset. This process generated a random matrix
 216 with an excess of zeros but the same magnitude of across- and within-row variation in link strength as the
 217 original data. Then I drew 100 groups by first drawing an individual and then its associates based on that
 218 matrix. From these 100 groups, I computed dyadic co-occurrence frequencies. These frequencies represented
 219 the final link strength of the simulation. Compared to the initial Erdős–Rényi graph, some links were created
 220 and some disappeared during the group drawing process. In both tests, I computed the Mahalanobis distance
 221 between the simulated and observed \mathcal{C}_ω and \mathcal{C}_g scores. The Mahalanobis distance M measures the distance
 222 between a point P (here, the two observed dissimilarity scores \mathcal{C}_ω and \mathcal{C}_g) and a distribution characterized

223 by a mean P_0 and a variance-covariance matrix S , according to the formula $M = \sqrt{(P - P_0)^T \cdot S^{-1} \cdot (P - P_0)}$. I
 224 computed P_0 and S from the cloud of simulated C_ω and C_g values. I then assessed the Mahalanobis distance
 225 against the chi-squared distribution with two degrees of freedom.

226 If test A was not significant, I concluded that the dissimilarities were explained by variation in individual
 227 frequencies in the dataset, i.e., the dissimilarities were not large. If test B was not significant, I concluded that
 228 the dissimilarities were large but mostly explained by missing links, rather than by the variation in the
 229 strength of existing links. If both tests A and B were significant, I concluded that there was either an excess of
 230 weak triplets closed by one strong link or an excess of balanced triangles made of three equally strong links,
 231 which an examination of the ω and g scores could decipher.

232 I also devised a test that focused on the lack of “forbidden triads” *sensu* Granovetter, i.e., strong triplets
 233 closed by a weak link. For this test C, I simply shuffled the link strengths while conserving other network
 234 aspects (Opsahl et al., 2008). I recomputed the ω and g scores after the shuffle. I used a chi-squared test with
 235 four degrees of freedom to determine whether the observed quadrant distribution differed from the expecta-
 236 tion from shuffled networks. I expected a significant lack of triads in quadrant 3 (“forbidden triads”). This
 237 could also complete tests A and B by pointing out whether quadrant 1 (balanced triangles made of three
 238 equally strong links) or quadrant 2 (weak triplets closed by one strong link) were in excess.

239 I compared the new transitivity scores across studies using linear mixed models with the
 240 logit-transformed C_ω and C_g as dependent variables and the logit-transformed edge density as predictor.
 241 Because the occurrence of modules of individuals that interact more amongst themselves than with the rest of
 242 the network could be the cause of triad-level dissimilarities, I also considered the additive effect of the net-
 243 work modularity.

244 1.7. The fragmentation of the subnetwork of strong ties

245 After having delineated the aforementioned modules (see section 1.1), I computed the *fragmentation* score
 246 as the overall network size divided by the average size of the modules that contained more than one individ-
 247 ual. If the score is high, the network is fragmented into a large number of small modules, and inversely. I used
 248 notation \mathcal{F}_w and \mathcal{F}_0 for the weighted and unweighted versions of the fragmentation score, respectively. \mathcal{F}_w
 249 is computed when the community-finding algorithm accounts for link strength and \mathcal{F}_0 is computed when it
 250 does not. I then computed the fragmentation ratio $\frac{\mathcal{F}_w - \mathcal{F}_0}{\mathcal{F}_0}$. The ratio quantifies how much more fragmented the
 251 subnetwork of strong links is, compared to the network as a whole (Appendix S2 for a simulation). A large
 252 ratio indicates that strong links occur in many small modules, e.g., there is more than one module of strong
 253 links in each module of weak links (a module can contain a single link and two individuals). A small ratio
 254 indicates that there is on average about one module of strong links embedded in each module of weak links.
 255 A negative ratio indicates that some of the modules do not feature any strong link. In other words, the frag-

256 mentation ratio $\frac{F_w - F_0}{F_0}$ increases when the subnetwork made of only the stronger ties is more fragmented
 257 than the network as a whole. I predicted that this ratio should be positive and increase with the edge density.
 258 I tested these predictions using a linear model with the fragmentation ratio as the dependent variable and the
 259 logit-transformed edge density as predictor.

260 2. Results

261 2.1. Verifying the natural transitivity of strong links

262 The weighted transitivity score C_1 was on average larger than the unweighted score C_0 but only by 2%
 263 (\pm SD: 6%) (Table 1). This suggests that strong triplets were too rare to influence the computation of C_1 (cf. next
 264 section).

265 In the second test, as I removed an increasing proportion of the weakest links, there was moderate evi-
 266 dence that the transitivity increased more than the edge density (Fig. 1a; McFadden's $r^2 = 0.06$). Statistically
 267 speaking the effect was however significant (likelihood ratio test against the intercept-only model: $df = 8.3$,
 268 deviance = 6.3, F-test $P < 0.001$). The evidence mostly came from networks of intermediate initial edge density
 269 (Fig. 1a: grey polygon; likelihood ratio test against the model without the interaction: $df = 7.7$, deviance = 5.8, P
 270 < 0.001 , McFadden r^2 for the interaction = 0.04). The predicted increase in b from about 0.45 to 0.6 (grey curve)
 271 would translate in approximately a +0.08 gain in transitivity. Thus, the increase in transitivity with Q was
 272 moderate on average across studies. However, the increase was clear-cut in at least some of the studies (e.g.,
 273 Fig. 1b).

274 2.2. The rarity of strong links

275 56% of the studies reported distributions of link strength that were more inegalitarian than a uniform
 276 distribution (Fig. 2). However, most of the dense networks exhibited inegalitarian properties, as the Gini coef-
 277 ficient increased with the edge density (Wald's $Z = 4.8$, McFadden's $r^2 = 0.3$, ANOVA: $P = 0.002$; Fig. 2). In other
 278 words, strong links were rarer in dense than sparse networks.

279 2.3. Dissimilarity between the three links in each triadic relationship

280 As the edge density increased, the networks dissimilarity scores went from quadrant 4 (mostly false tri-
 281 plets) to quadrant 1 (mostly balanced triangles) through quadrant 2 (mostly weak triplets closed by one strong
 282 link) while avoiding quadrant 3 (mostly strong triplets closed by one weak link; "forbidden triad") (Fig. 3).
 283 Triplets in quadrants 1 and 2 were more frequent and quadrant 3 was rarer than expected from shuffled net-
 284 works (test C) (Fig. 3). There was strong evidence that the excess of quadrants 1 and 2 was due to the occur-
 285 rence of distinct modules, because both the C_w and C_g score correlated with the network modularity, even
 286 after accounting for the edge density (respectively, $Z = -0.5$, $r^2 = 0.01$, $P = 0.001$ and $Z = 6.2$, $r^2 = 0.43$, $P < 0.001$;
 287 Table 1). The C_w and C_g scores nevertheless captured information neither conveyed by the modularity score
 288 nor by the usual transitivity score (Appendix S3).

289 In most studies, including all the studies that involved more than 35 individuals, both permutation tests A
290 and B were positive (Table 1). This confirmed that the excess of quadrants 1 and 2 was not due to links missing
291 at random or to variation in individual frequency of occurrence. Yet, in a few studies, the dissimilarities were
292 as expected under one of the null models. In networks that were both small and dense, I found no evidence
293 that the triads were any different from those of a full network (Table 1: *Poecila reticulata*, *Macaca assamensis*,
294 *Macaca fuscata*: $P_A > 0.05$). In the proximity logs of barn swallows *Hirundo rustica*, of one of the subpopulations of
295 elk *Cervus canadensis*, and in the Nilgiri langur *Trachypithecus johnii*, the triadic dissimilarities could apparently
296 be created by links missing at random ($P_B > 0.05$).

297 2.4. The fragmentation of the subnetwork of strong ties

298 Accounting for link strength increased the fragmentation score on average by 35% (\pm SD 50%) (Fig. 4 and
299 Fig. 1b: average fragmentation ratio 0.35). The fragmentation ratio increased with edge density ($Z = 2.3$, $r^2 =$
300 0.09 , $P = 0.003$; Fig. 4). These results mean that most modules featured at least one strong link; and that within
301 each module, strong links tended to be isolated or to form several small clusters rather than to occur as a single
302 cluster of strong links per module. The phenomenon increased in intensity as the network edge density in-
303 creased.

304 3. Discussion

305 By reanalyzing 26 published datasets of animal association networks, I first retrieved a major result of the
306 field, namely that strong links are more transitive than weak links (Fig. 1). However, the effect was maybe not
307 as strong as expected. My explanation is that, in many of the studied networks, even the strongest associations
308 were not strong enough to mechanistically force transitivity. In addition, a few of the networks that I included
309 feature minimal variation in link strength. Nevertheless, in the studies that were not affected by any of these
310 two issues, the increase in transitivity with link strength was clear-cut (e.g., Fig. 1b). Next, I observed three
311 ways in which the frequency and position of strong links offset their natural transitivity. First, strong links
312 became rarer as the edge density and overall transitivity increased (Fig. 2). Second, the three links in each
313 triangle were mostly dissimilar, more dissimilar than expected, and increasingly dissimilar as the edge density
314 and overall transitivity increased (Fig. 3). Third, the subnetworks of strong links were increasingly fragmented
315 as the edge density and the overall transitivity increased (Fig. 4). These results do not challenge the strength of
316 weak ties paradigm (Granovetter, 1973). Indeed the paradigm described some of the networks very well (Fig.
317 1b). However, in many of the included studies, most ties were weak, making the strength of weak ties a
318 somewhat tautological property.

319 These results may help explain why cooperative behaviors are not more widespread than they are among
320 group-living vertebrates. First, cooperation requires stable relationships (Nowak, 2006; Teunissen et al., 2021). I
321 found these to be increasingly rare as the overall gregariousness, the number of association partners, increased

(Fig. 2). This suggests that vertebrate social groups can either be dense or stable. Upper limits on the number of simultaneous partners, or a negative effect of existing relationships on the probability to create new ones, might be involved (Dávid-Barrett & Dunbar, 2013; Stadtfeld et al., 2020). Second, I found that stable transitive motifs were fewer and smaller than what they could have been. Compared to intransitive networks, stable transitive motifs offer more pathways for the benefits of collaboration to be collected, e.g., via indirect reciprocity (Block, 2015) and contributions towards common goods (Mielke et al., 2019). Stable transitive motifs might also facilitate the policing and coercion of selfish associates for the same reasons. The scarcity and small size of stable transitive motifs would not help cooperative behaviors to emerge. Overall, my observations help explain why many group-living vertebrates do not exhibit advanced cooperative behaviors, or why cooperative behaviors are rarely expressed. Note however the alternative interpretation that stable transitive motifs may be rare and small *because* cooperation does not bring enough benefits. In addition, as mentioned earlier, a functional response is also possible, in which individuals navigate their social environment in a way that is analogous to the way resource selection occurs in the physical environment (Holling, 1959). More precisely, the marginal benefit of an additional stable relationship might decrease with the number of pre-existing stable relationships, leading to a concave relationship between the number of potential partners (as proxied by the edge density) and the selection of specific partners. Formal tests would require dynamic data rather than aggregated data, so that a dynamic model of link creation, stability, and activation can be fitted, while taking individual attributes such as kin relationships into account (e.g. Snijders et al., 2010).

Importantly, the patterns that I report do not necessarily emerge from individual decisions alone. Environmental and demographic variation clearly contribute to network structure. For example, the fragmentation ratio changed from -0.3 to +2.1 between a dense subpopulation and a sparse subpopulation of elk *Cervus canadensis* (data: Webber & Vander Wal, 2020). On the other hand, the observed patterns can be created by relatively simple social behaviors. Kin-biased associations in particular, especially between mother and offspring, and associations between breeding male and female, can cause an excess of weak triplets closed by one strong link (Péron, 2022). This point is important because different species have different hard-wired socio-spatial structures, e.g., in most mammals, offspring form strong bonds with their mothers that may last past weaning age, whereas in birds the dominant bond may be between the male and female of a pair. In other words, the patterns that I report stem from a wide variety of mechanisms. Some are environmental constraints, some are species-specific evolved social strategies, and others represent individual reactions norms.

In terms of caveats, a major one is that the datasets are not representative of all vertebrate social systems. First, the literature is biased towards small group sizes, which are easier to monitor. Besides that, social network methods are not compulsorily used on the most social species. For example, the association network of lionesses *Panthera leo* can appear trivial because association is almost obligate within a pride and almost forbidden across prides. Yet, it is in this context that the strength of weak ties paradigm applies the most (Craft et

356 al., 2011), that the transitivity expectedly increases the most with link strength, and that cooperation is ex-
 357 pectedly the most beneficial.

358 Another caveat is that the criteria to determine what constituted an association undoubtedly influenced
 359 the recorded network structures (Gazda et al., 2015). For example, the network drawn from the ritualized
 360 embraces of brown spider-monkeys *Ateles hybridus* (Rimbach et al., 2015) was one of the few that scored almost
 361 into quadrant 3 (the “forbidden triad”; Fig. 3). This specific type of association lasts less than a minute
 362 (Rimbach et al., 2015). This would expectedly relax the physical constraint that strong links are compulsorily
 363 transitive. This suggests that the triadic dissimilarity scores C_ω and C_g can perform as an indicator of the
 364 intransitivity of strong links. Ritualized embraces may obey a principle of preferential attachment to keystone
 365 individuals (Range & Noë, 2005; Schino, 2001), which would create strong triplets featuring a keystone in the
 366 middle, closed by weak or no links between the subordinates. The rudimentary permutation tests A and B are
 367 however not suited to formally test such hypotheses. Here also, formal tests would require dynamic data ra-
 368 ther than aggregated data. Nevertheless, the statistics developed for this study captured information not
 369 summarized in other network-level metrics (Appendix S3). They can therefore help quantify the socio-spatial
 370 structure of different species and populations, the extent to which this structure favors the evolution of coop-
 371 eration, and the social network response to changes that influence the costs and benefits of sociality.

372

373 **Supplementary Materials:** Appendix S1: R script to compute the dissimilarity-weighted transitivity scores and to perform
 374 the quadrant and distance tests. Appendix S2: Simulation study supporting the use of the fragmentation ratio to quantify
 375 whether the subnetwork of strong links is more fragmented than the network as a whole. Appendix S3: Principal compo-
 376 nent analysis.

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384

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514

515 **Tables**

516 Table 1: Overall results of the weighted network analysis for the 26 species. Given are the taxonomic order, the type of
 517 association ($ty = GM$: shared subgroup membership, PR: spatial proximity, CO: physical contact), the number of study
 518 individuals N , the edge density \mathcal{D}_0 , the modularity \mathcal{M} , the variance in rescaled edge weights Var , the Gini coefficient of
 519 inequality in link strength G , the fragmentation ratio FR quantifying the fragmentation of the subnetwork of strong links
 520 relative to the network as a whole, the unweighted transitivity coefficient \mathcal{C}_0 , the transitivity coefficient weighted for
 521 triplet strength \mathcal{C}_1 , and the triadic dissimilarity scores \mathcal{C}_ω and \mathcal{C}_g . “q.” gives the quadrants that were more frequent than
 522 expected in test C. “Ref.” is the original study and “ASNR” is the reference number in “A social network repository” (Sah et
 523 al., 2019; <https://bansallab.github.io/asnr/about.html>).

524

525 **Figure legends**

526 Fig. 1: (a) Model predictions illustrating that, when an increasing proportion of the weakest links is removed (x-axis), the
 527 network transitivity \mathcal{C}_0 is increasingly larger than expected from the edge density \mathcal{D}_0 (y-axis). (b) Raw data for a single
 528 population. The data document group membership in a killer whale (*Orcinus orca*) population (Weiss et al. 2020). Thick
 529 black lines indicate the 10% strongest links.

530 Fig. 2: The Gini coefficient (y-axis) increases with the edge density \mathcal{D}_0 of the network (x-axis). The color scale corresponds
 531 to the transitivity score \mathcal{C}_0 . The Gini coefficient is a measure of dispersion based on the pairwise differences in link strength
 532 among all the connected dyads in the network. The highest Gini coefficient in the present study (acorn woodpecker
 533 *Melanerpes formicivorus*; data: Shizuka et al., 2022) means that 95% of the recorded associations occurred between 5% of the
 534 connected dyads. The dashed line corresponds to the null hypothesis that the distribution of link strength is uniform.

535 Fig. 3: (a) Graph-level triadic dissimilarity scores \mathcal{C}_g and \mathcal{C}_ω in 26 species (see methods for the definition). The color scale
 536 corresponds to the edge density \mathcal{D}_0 . The grey outline delineates the domain of possible (ω, g) values. The pictograms
 537 represent the six extreme cases of triads. *Triplets* correspond to triads where one individual A is associated with two dif-
 538 ferent individuals B and C. If the triplet is closed by a link between B and C, it is called a *triangle*. If the three links in the
 539 triangle are equally strong, the triad falls in the lowerleft corner of the plot. Different triangular configurations correspond
 540 to different other sections of the plot, a delineated by the four quadrants 1 to 4. A *false triplet* is a triad made of a dyad plus a
 541 disconnected singleton, corresponding to the rightmost part of the plot. (b) Triad-level dissimilarity scores summarized
 542 over two categories of edge density and over the four quadrants. The black outline indicates the expected distribution from
 543 test C, demonstrating the lack of “forbidden triads” (quadrant 3) and the excess of triangles where the closing link is strong
 544 (quadrant 1 and quadrant 2).

545 Fig. 4: The fragmentation ratio (y-axis) increases with the edge density \mathcal{D}_0 of the network (x-axis). The color scale corre-
 546 sponds to the transitivity score \mathcal{C}_0 . The fragmentation ratio is the proportional difference between the weighted and un-
 547 weighted fragmentation scores. The highest fragmentation ratio in the present study (a low density population of elk
 548 *Cervus canadensis*; data: Webber & Vander Wal, 2020) means that the weighted network was 3 times more fragmented than
 549 the unweighted network.

550